MULTISPECIES AGE-STRUCTURED ASSESSMENT

MODELING AS A TOOL OF FISHERIES MANAGEMENT

IN THE GULF OF ALASKA

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August 10, 2012
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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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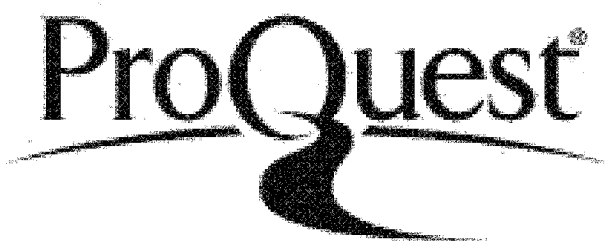
Fairbanks, Alaska

August 2012



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ABSTRACT

A multispecies age-structured assessment model (MSASA) for the Gulf of Alaska (GOA) is developed to examine the effects of integrating predation mortality into stock assessment efforts. Age-specific predation mortality is modeled as a flexible function of predator and prey abundances, constructed from species-preference and size-preference parameters and fitted to stomach-content data. Modeled species include arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). Recruitment, residual natural mortality, full-recruitment fishing mortality, and fishery/survey selectivities are estimated for pollock, cod, and flounder; abundances for apex predators sea lions and halibut are input. Estimated trophic structures and predation links show significant changes as a result of the inclusion of higher trophic level predators, and model results are highly sensitive to assumptions regarding sea lion diet. Simulation exercises suggest that model performance degrades more due to model misspecification and data scarcity than assumptions regarding data weighting and variance. Estimates of predation mortality work in tandem with survey data, constraining predation estimates in the face of incomplete diet data and potentially improving estimates of cohort structure. Exploration of predator functional responses (PFR) shows the default GOA MSASA Holling Type II PFR to be more flexible than initially thought, and that explicitly modeling predator competition for the same prey can improve model fit to stomach-content data. Median parameter estimates and their respective variances from the fitted MSASA model are used to construct management

strategy simulations. Reducing fishing pressure on pollock during periods of high predator biomass is less effective at preserving pollock stocks than raising fishing pressure on flounder, and multispecies harvest control rules and biological reference points are shown to be more conservative and more efficient at preserving stock abundance while maintaining catch levels than their single-species counterparts.

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ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Terrance J. Quinn II for his expertise in the field of fisheries population dynamics, and his patience in working with me. I also thank my committee members Drs. Jeremy Collie, Franz Mueter, Gordon Kruse, and Keith Criddle. My deep appreciation is given to Dr. Teresa A'mar for her endless revisions, suggestions, and assistance with coding. Dr. Jim Ianelli provided me with the initial code structure for model development, and Dr. Geoff Lang was kind enough to extract the relevant stomach data from the NOAA database for my use.

The Trifecta of Perfection at the Juneau School of Fisheries and Ocean Science is composed of the administrative support team: Gabrielle Hazelton, Debi Rathbone, and Louisa Hayes. Without their assistance and humor, nothing would have been accomplished.

This work was funded in part by the Pollock Conservation Cooperative Research Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the Center or the University of Alaska.

This publication is also the result of research sponsored by Alaska Sea Grant with funds provided by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-11, 14), and from the University of Alaska with funds appropriated from the State.

This publication is also the result in part of research and education sponsored by the Cooperative Institute for Arctic Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA17RJ1224 with the University of Alaska.

GENERAL INTRODUCTION

Fisheries managers often utilize statistical models to examine the dynamics underlying observations of abundance and cohort structure. These models are intended to encompass major system dynamics as well as being robust to uncertainty from sampling, observation, and process. Traditional single-species models, in which system variables affecting abundance are represented by mortality and recruitment parameters (Quinn and Deriso 1999, Quinn and Collie 2005), are currently being expanded into forms capable of explicitly modeling ecosystem processes (Marasco et al. 2007) and that contain time-varying parameters for realism (Sainsbury 1998, Wilberg and Bence 2006). Fueled by an increased understanding of complex ecosystem dynamics and coupled with expanded computing resources, this study has as its primary aim to reduce the statistical uncertainties involved in stock assessment modeling and, by association, the economic and ecological risks inherent in implementing fisheries management strategies.

A primary focus in the efforts to improve models has been the replacement of a constant natural mortality with an age and/or time-specific natural mortality (Fu and Quinn 2000). Traditional single-species stock assessment models include predation mortality under the umbrella of natural mortality, with total mortality being the sum of fishing and natural mortalities. The assumption of time-invariance with regards to natural mortality may bias the results of fisheries models and the management decisions based upon them. Predation can affect prey abundance and production far more than fishery removals (Bax 1998) and accounts for the vast majority of non-fishing mortality for non-

apex species (Gaichas 2010). Explicitly including predation in fisheries models can reduce the bias contained in the assumption of a constant natural mortality, and illuminate some of the complex relationships between species that drive the population dynamics of a given system.

The awareness that fisheries removals have the ability to profoundly alter the structure and dynamics of marine systems has been developing for a number of years (Pauly et al. 1998), and this awareness, along with observed reductions in catch, has resulted in a gradual movement in management bodies towards ecosystem-based fisheries management (EBFM) (Marasco et al. 2007). Evaluating and quantifying predator-prey relationships and the effects that fisheries removals have upon them is fundamental to this movement. Reduction in older cohorts from overfishing can lead to increased gear selectivity for younger age-classes (Myers and Quinn 2002), yet predation studies show that these same younger age-classes also experience the highest predation pressure (Hollowed et al. 2000a, Jurado-Molina et al. 2005). A population most likely cannot sustain escalating mortality from multiple sources, increasing the likelihood of collapse (Hartman and Margraf 2003).

Predation has been successfully modeled in a single-species context (Livingston and Methot 1998, Hollowed et al. 2000a, Moustahfid et al. 2009), but a multispecies approach has generally been shown to have better statistical fit to data, to improve estimates of mortality and recruitment, and to provide a better framework for analysis of predation than single-species models (Hollowed et al. 2000b, Tsou and Collie 2001). Given their

complexity, however, multispecies models have not yet replaced single-species models but are sometimes used in an auxiliary capacity (Turnock et al. 2007, Dorn et al. 2008).

A multispecies age-structured assessment (MSASA) model for the Gulf of Alaska (GOA) was originally developed by Van Kirk et al. (2010), modeling predation dynamics among three species with significant predator-prey interactions: walleye pollock (*Theragra chalcogramma*), arrowtooth flounder (*Atheresthes stomias*), and Pacific cod (*Gadus macrocephalus*). The current work seeks to expand, refine, and test this model to prepare it for formal integration into stock assessment efforts. Chapter 1 expands the original three-species model into a five-species model through the inclusion of apex predators Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). These five species account for the majority of pollock predators in the Gulf of Alaska. Chapter 2 uses Monte Carlo simulations to assess model performance and the robustness of parameter estimates in the face of data limitations and model mis-specification. Chapter 3 evaluates the effects of varying ingestion rates on population dynamics, and examines a series of alternative predator functional responses; accurately modeling predation mortality depends upon accurately modeling the behaviors by which predators execute those removals. Finally, in Chapter 4 the refined model is used to generate potential multispecies biological reference points and harvest control rules which are implemented in a series of management strategy evaluations.

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CHAPTER 1

MULTISPECIES AGE-STRUCTURED ASSESSMENT FOR GROUNDFISH AND SEA LIONS IN ALASKA[1]

[1] Van Kirk, K.F., T.J.Quinn II, J.S. Collie, and Z.T. A'mar. 2012. Multispecies age-structured assessment for groundfish and sea lions in Alaska. In: G.H. Kruse, H.I. Browman, K.L. Cochrane, D. Evans, G.S. Jamieson, P.A. Livingston, D. Woodby, and C.I. Zhang (eds.), Global Progress in Ecosystem-based Fisheries Management. Alaska Sea Grant, University of Alaska, Fairbanks.

ABSTRACT

The current push towards ecosystem-based fisheries management, in conjunction with the limited application of current multispecies models in that context, outlines the need for a more holistic approach that explicitly includes age-structured species interactions. To meet this need, a multispecies age-structured assessment model (MSASA) for the Gulf of Alaska was expanded from three species (arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Theragra chalcogramma*)) to include two major high trophic level predators as external inputs: Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lions (*Eumatopias jubatus*). Inclusion of the large predators resulted in increased predation on older prey ages, including those fully recruited into the commercial fishery. Significant changes to trophic structures and predation linkages from the core model were observed. Estimation of residual natural mortality M_0 was achieved through modification of survey selectivity curves and survey catchability Q values from the core model. Predation mortality, survey selectivity, and M_0 are confounded in their relationship to determining cohort structure. The MSASA model structure is able to track complex population dynamics, but variability in parameter estimates makes clear the need for improved stomach-content data.

KEYWORDS: multispecies, predation, Gulf of Alaska, walleye pollock, arrowtooth flounder, Pacific cod, stock assessment, Pacific halibut, Steller sea lion

INTRODUCTION

The application of mathematical modeling to marine ecosystems is an attempt to explain observable data by the modeling of unobservable processes (Anderson 2009). Predation mortality is one of the most important of these processes, as it affects every organism in marine systems and can exceed fishing mortality for commercially fished species (Bax 1998, Gaichas et al. 2010). Integration of predation into stock assessments is a fundamental aspect of ecosystem-based fisheries management (EBFM) (Marasco et al. 2007). Multispecies Virtual Population Analysis (MSVPA) and mass-balance models such as ECOPATH (Christensen et al. 2000) are currently used by fisheries managers in an advisory capacity but have yet to be fully integrated into stock assessment methods.

Natural mortality M refers to mortality from sources other than the commercial fishery, and has generally been assumed constant in single-species stock assessments and fishery models (Quinn and Deriso 1999). Andersen et al. (2009) and Andersen and Beyer (2006) examined the relationship between natural mortality and growth, and suggested that predation accounts for the entirety of natural mortality for non-apex marine species. Gaichas et al. (2010) concluded that predation constituted the majority of mortality for pollock in the Gulf of Alaska (GOA), and that the assumption of a constant natural mortality was erroneous. By separating M into a variable predation mortality P and a residual natural mortality term M_0, model realism is increased and the bias arising from the assumption of a constant natural mortality M is reduced.

Predation mortality, as a major component of *M,* is confounded with estimates of survey selectivity (Thompson 1994) when estimating cohort structure and abundance. Stock assessment estimates of total natural mortality *M* are sometimes conditioned on assumed selectivity curves (e.g., Turnock and Wilderbauer 2009). Fisheries management depends on the estimation of age-specific predation mortality to define appropriate biological reference points for species subject to heavy predation (Collie and Gislason 2001, Tyrrell et al. 2011), to quantify the cascade of commercial fishery effects through the system, and to provide a more accurate assessment of the population structure from which commercial catch is drawn.

The current work expands an existing multispecies age-structured assessment (MSASA) model for the Gulf of Alaska (Van Kirk et al. 2010) from three species (walleye pollock (*Theragra chalcogramma*), arrowtooth flounder (*Atheresthes stomias*), and Pacific cod (*Gadus macrocephalus*)) to five by the addition of Pacific halibut (*Hippoglossus stenolepis)* and Steller sea lion (*Eumetopias jubatus*). Mass-balance models show these species to be among the top predators of pollock larger than 20 cm (ages 2+ in the current work) (Aydin et al. 2007). Age-1 pollock are targeted by a number of different predators, but Aydin et al. (2007) showed that arrowtooth flounder and cannibalism remain the largest two sources of predation mortality for all ages of pollock in the GOA. Including these major pollock predators moves the MSASA model closer to a "minimal realistic model" (Punt and Butterworth 1995) in which the major species interactions affecting pollock abundance have been explicitly modeled, allowing practical application to fisheries management.

Predation in the original three-species MSASA model was observed to be disproportionately high on younger prey age-classes, due in part to the enormous abundances of younger ages and in conjunction with the similar sizes of the three modeled species, which limits the number of prey able to be consumed and digested. Larger predators, however, may bring increased pressure on older cohorts. As cod have no modeled predators in the original model but are a major prey of Steller sea lions, the inclusion of sea lion in the model may alter overall system population dynamics and structure by exerting predation pressure on what was previously a model apex predator.

METHODS

Core Model

Van Kirk et al. (2010) described the core GOA MSASA model (equations 1.1 – 1.3 below were taken from that manuscript). In overview, standard equations of single-species stock assessment models (Quinn and Deriso 1999) were used to model year-class propagation, commercial catch-at-age, and fishing mortality. Total instantaneous mortality Z was decomposed into fishing mortality F, predation mortality P, and a residual natural mortality term M_0.

Predation mortality was a function of predator and prey abundances, estimated from size- and species-preference parameters in conjunction with annual ingestion requirements. As different datasets used different measures of size (length or weight),

both length and weight were mapped to age by the application of externally defined length-at-age and weight-at-age bins constructed from the Alaska Fisheries Science Center (AFSC) Stock Assessment and Fishery Evaluation (SAFE) reports; model equations used the age subscript a for prey species and b for predator species. Predation mortality P was defined as

$$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_{j} \sum_{b} I_{j,b} N_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} \tag{1.1}$$

in which $I_{j,b}$ was the annual ration for a given predator of species j, age b, $N_{j,b,t}$ was the abundance of predator j,b at the beginning of year t, and $B_{i,a,t}$ was the biomass of prey species i, age a at the beginning of year t. The ratio $\phi_{i,a,j,b,t} / \phi_{j,b,t}$ was the proportion of prey i,a in all food available to predator j,b in year t, assumed equal to the proportion of food within the stomach of predator j,b composed of prey i,a in year t, and defining the overall preference of predator j,b to feed upon prey i,a in year t. The numerator $\phi_{i,a,j,b,t}$ was termed "suitability", as

$$\phi_{i,a,j,b,t} = \rho_{j,i} g_{i,a,j,b} B_{i,a,t} \tag{1.2}$$

in which $\rho_{i,j}$ defined the preference of predator j to feed on species i, and $g_{i,a,j,b}$ defined the optimal prey size i,a selected by predator j,b. The size-preference g of predator j,b was modeled as a lognormal function following Anderson and Ursin (1977):

$$g_{i,a,j,b} = \exp\left[-\frac{1}{2\sigma_j^2} \left(\ln \frac{w_{j,b}}{w_{i,a}} - \eta_j \right)^2 \right] \tag{1.3}$$

in which σ and η were size-preference parameters specific to each predator j, and w was the weight-at-age for each age of predator or prey.

The core model made a number of assumptions, designed to limit model complexity while having minimal qualitative impact on parameter estimates. These included temporally invariant length/weight-at-age, gear selectivity, survey catchability Q (set to 1), and predator annual ration. Abundances were annually estimated over years 1981 to 2001. Data for model fitting via maximum likelihood methods using AD Model Builder (Fournier et al. 2011) included commercial catch and survey abundance taken from SAFE reports, and stomach-content data supplied by the Resource Ecology and Ecosystem Modeling (REEM) database of the AFSC. (General information on stomach data collection and processing can be found in Yang and Nelson 2000; relevant data were obtained courtesy of G. Lang, AFSC.) Model estimates of commercial catch and survey indices, along with annual abundance trends, were consistent with stock assessments produced by the AFSC (Dorn et al. 2010, Thompson et al. 2010, Turnock and Wilderbuer 2009), and predation curves were in general agreement with similar research (Hollowed et al. 2000), confirming model functionality.

Expanded Model

The International Pacific Halibut Commission (IPHC) regulatory areas falling within the Gulf of Alaska are areas 3A, 3B, and 2C. Abundance-at-age data for area 3A were supplied by the IPHC and used as indices for abundances in areas 3B and 2C

following the relative bottom-area covered by each region; abundances for halibut are fixed model inputs. Ages of modeled halibut run from 8 – 20+ years. Weights-at-age were supplied by the IPHC. As halibut growth has exhibited a drastic decline since the early 1980s, annual mean weights-at-age are used instead of making the assumption of a constant mean weight-at-age as applied to pollock, cod and flounder in the core model.

Mean weight-at-age has a significant effect on predation, as the ratio between predator and prey weight is integral to its estimation (eq. 1.3). The core model used a single set of size-preference parameters for each species, with the assumption that size-preference is a constant function of gape and physiology; changes in predation in response to strong or weak year classes of prey are better modeled through explicitly coded predator functional response. The continual change in halibut size, however, implies changes in size-preference, and three sets of time-specific size-preference parameters were estimated.

Annual ingestion rates were calculated following Aydin et al. (2007). The von Bertalanffy growth equation was used to determine the relationship between the change in weight and total rate of energy assimilation and the rate of energy loss as:

$$\frac{dW}{dx} = HW^{d} - KW^{n}, \tag{1.4}$$

in which H, d, n, and K are parameters that define the allometric relationship between age and weight as a function of the generalized von Bertalanffy equation, x is age, and W is the weight-at-age; parameter H is the key parameter related to ingestion. Aydin et al. (2007) accepted the suggestion of Essington et al. (2001) that n can be set to 1 with the

assumption that respiration and body weight have a linear relationship, and by setting the differential in eq. (1.4) to zero, obtained an expression for the asymptotic weight W_∞ as:

$$\left(\frac{H}{K}\right)^{1-d} = W_\infty . \tag{1.5}$$

Following the method of Essington et al. (2001) produces:

$$W_x = W_\infty \left(1 - e^{-K(1-d)(x-x_0)}\right)^{1/1-d}, \tag{1.6}$$

in which x_0 is the age at which the weight of the organism is assumed to be zero. Meta-analysis work with predator-prey species in the North Pacific allowed Aydin et al. (2007) to arrive at a value of 0.8 for *d*. Using field studies to set values for weight at age, eq. (1.6) can be used to solve for W_∞, K, and t_0. Solving eq. (1.6) for halibut is problematic, however, as W_∞ and K are correlated, and the rapid shift in halibut growth over time has made parameter fitting difficult. Age of maturation, however, has remained constant, and it was determined that the ratio of weight at 50% maturity (age 11-12) to W_∞ in the early 1990s was 0.4561 (S. Gaichas, Alaska Fisheries Science Center, Seattle, Washington, pers. comm., 2010). Applying this ratio to the weight-at-age data produced a value for W_∞ that was 1.159% greater than the weight at age 20; this percentage was used to generate annual values for W_∞. Values for K and x_0 were estimated for each year by fitting eq. (1.6) to observed weights-at-age for ages 8 – 19; as age 20 is a plus group and thus carries a potentially skewed weight, it was omitted. Then, from eq. (1.5), the solution for H is:

(1.7) $$H = Kw_{\infty}^{0.2},$$

producing an estimate of annual ingestion rate in kilograms consumed for each halibut of age *b* as:

(1.8) $$I_b = \frac{H}{A} W_b^d$$

in which *A* is a scaling parameter to compensate for consumed biomass that is indigestible, set through meta-analysis to 0.6 (Aydin et al. 2007).

Stomach-content data for halibut were supplied by the AFSC REEM program. Of the modeled species, pollock were the most significant prey item in halibut stomachs, followed by arrowtooth flounder, and although some individuals consumed cod, these were infrequent and the data were considered insufficient to provide adequate model forcing. Pollock and flounder are therefore the only modeled prey species for halibut. Stomach data from all sampled individuals within a given year were pooled to show the mean proportion of aggregate prey-at-age weight relative to total aggregate stomach weight for each predator-at-age. A single halibut was considered a sample of one, regardless of the number of prey items contained in its stomach. The total sample size, reflecting predators whose stomach contained pollock or flounder, was 398.

Stomach data were available for 1990, 1993, 1996, and 2001. Data were predominantly gathered in summer months but assumed to represent annual feeding behavior. Estimated halibut stomach-content values were averaged over the first ten years of model run (1981 – 1990) and fitted to the stomach data from 1990; data for 1993 and 1996 were merged and used to fit model estimates averaged over 1991 – 1996, and the

2001 data were used to fit model estimates averaged over 1997 – 2001. This approach was also used in the core model, in which stomach-content data were grouped into three seven-year blocks (Period 1: 1981 – 1987; Period 2: 1988 – 1994; Period 3: 1995 – 2001). Data sparsity did not allow fitting to each individual year, even where data for a given year existed; averaging over a set of years enabled more robust estimation of predation parameters, and the species-preference coefficient ρ (eq. 1.2) changed for each time-block, facilitating predation sensitivity to predator-prey abundances. Pooled stomach contents were assumed asymptotically normal relative to increasing sample size; explorations utilizing alternative distributions, including log-normal and multinomial, were unsuccessful. Weightings in the objective function, following Hanselman et al. (2008), were set to the square root of the sample size. The objective function component was a minimized sum of squares.

Abundance data for sea lions were taken from National Marine Mammal Laboratory aerial non-pup survey counts in the GOA, available for 1976, 1985, 1989 – 1992, 1994, 1996, and 2000, and supplied by the AFSC. Observed abundances were multiplied by 1.1331 to compensate for missed animals (Loughlin et al. 1992). A life table (York 1994) and survival rates for males and females (Winship et al. 2002) were used to calculate abundances-at-age with the assumption of a gender-equal birth ratio. Annual pup abundances, assuming a single pup per nursing female, were estimated from maturity and reproductive rates (Winship et al. 2002). Reproductive rates were modified to reflect the decline in observed GOA populations by minimizing the sum of squared differences between the corrected non-pup survey counts and the summed estimated

abundances-at-age for years in which survey data exist. Annual ingestion rates for sea lions were assumed different for males, non-nursing females, and nursing females with pups younger than one year, and were taken from the extensive bioenergetic work of Winship et al. (2002). Bioenergetic needs for first-year pups (age 0) are included in the mother's ingestion rate. Weights-at-age are taken from Winship et al. (2001).

Age-classes are modeled from 1 – 13+ years. Age 0 animals are not modeled beyond estimation of their mother's increased ingestion needs as a function of nursing. While some animals continue to nurse until age 3, most have been weaned by age 2, and at age 1 have already begun to supplement nursing with hunting, reducing the drain on parental energy reserves. For convenience, it is assumed that pups aged 1 and above will forage independently and no longer nurse. Maturity and reproductive rates from Winship et al. (2002) are used to estimate the number of nursing mothers per age-class per year. Age 3 is considered the onset of reproductive maturity, and by age 6 all females are considered mature and capable of reproducing.

The literature on sea lion diets is often contradictory. The Marine Mammal Protection Act of 1972 prohibits the taking of live specimens, and much of the available data were gathered prior to the modeled years. Many of the data focus on general prey taxonomy and frequency of prey occurrence, either in examined stomachs or as indicated by the presence of otoliths and other bony parts in sea lion scat, and supply no information regarding prey or predator age, or proportion of a given prey species by weight or volume to the total prey consumed. While it had originally been intended to group sea lions into male, female, and nursing female groups, the structure of the

available stomach-content data made this infeasible, and consequently, sea lions are merged into a single group with weighted means for weight-at-age and ingestion-at-age. It is assumed that the consumed proportions of each modeled prey species remained constant over time. Upper and lower bounds are set for the total proportion of each modeled prey species in the estimated stomach-contents for each age of sea lion; penalties are incurred in the objective function only if estimated stomach-content values fall outside those bounds.

Trites and Calkins (2008) provide the most detailed evaluation to date of prey sizes and proportions of species consumed by males and females, from examination of sea lion scat contents recovered from gender-specific haul-outs. Sea lion consumption, averaged over gender, was found to be 28.5% gadids, 11% flatfish, and the remainder a mix of salmonids, rockfish, forage fish, and cephalopods. These proportions are used to define min/max acceptable stomach-content values: flounder: 5% - 11%; pollock: 11% - 28.5%; cod: 11% - 28.5%; penalties were incurred in the objective function when estimated stomach contents fell outside these bounds. The large variation in the previous studies of Steller sea lion predation precluded any definition of size-preferences in the objective function stomach-content matrices.

Model estimates of sea lion stomach contents for each combination of predator age and prey age and species are averaged over all modeled years and fit between the minimum and maximum values in the objective function. As pollock appear to be the most commonly reported primary prey item for sea lions (Pitcher 1981, Merrick and Calkins 1996), size-preference (eq. 1.3) is bound by minimum and maximum pollock

weights-at-age. Although sea lions are capable of tearing apart and consuming large prey in smaller pieces, general observation suggests that most sea lions manipulate fish prey in the mouth to facilitate complete ingestion without tearing (S. Atkinson, Juneau School of Fisheries and Ocean Sciences, Juneau, Alaska, personal communication, 2010). As with other species, the majority of stomach-content data reviewed in the literature were gathered in summer and assumed seasonally-invariant.

Assumed stomach content distribution and objective function weightings are as other modeled species. For sea lions, the sample size is the sum of sample sizes over all literature reviewed, totaling 2,425.

The expanded model opened both residual natural mortality M_0 and survey catchability Q to estimation, whereas these were input into the core model. Core model assumptions regarding the shape of the selectivity curve were relaxed and alternatives for selectivity estimation were explored, including a double logistic curve, a normalized gamma density function, and a simple vector of point estimates for each age and species. Although additional catch, survey, and stomach-content data were available for the expanded model than for the core model, modeled years were deliberately limited to those from the core model for better comparison of results.

RESULTS

Initial runs of the expanded model were unable to reach convergence. As with other studies (Fu and Quinn 2000), Q and M_0 were confounded and inversely related:

reasonable values for M_0 were associated with unrealistically high values for Q, while setting Q values close to 1 as is commonly done in stock assessments (Dorn et al. 2010, p. 69, Thompson et al. 2010 pp. 166 - 167, Turnock and Wilderbuer 2009, p. 629) caused residual natural mortality rates to rise beyond acceptable values. As survey selectivity contains implicit assumptions regarding the underlying population structure (Thompson 1994), M_0 values were also affected by the choice of selectivity curves. Setting parameter bounds for Q and M_0 allowed for parameter estimation and model convergence, but these bounds were sufficiently restrictive that they were essentially no better than using input values. Fu and Quinn (2000) recommend setting values for Q while allowing estimation of M_0. Following their work, values for Q were set to those presented in the literature: flounder = 1.3 (Somerton et al. 2007), cod = 0.92 (Nichol et al. 2007, Thompson et al. 2010), pollock = 0.8 (Dorn et al. 2005). Survey selectivity-at-age values s_a from the core model were replaced by a normalized gamma density function for each species (Quinn and Deriso 1999)

$$s_a = \frac{a^{\alpha} e^{-\beta a}}{\max_j j^{\alpha} e^{-\beta j}}. \tag{1.9}$$

M_0 was also sensitive to new first-order predation effects from the addition of larger predators and $2^{nd}...n^{th}$ n-order effects from predation cascades. Final model values for M_0 were 0.353 for cod (a decrease fro$_{m\,0}$.37 in the core model), 0.277 for flounder (an increase from 0.2), and 0.2 for pollock (unchanged).

Objective function values generally improved from core model values, with the largest improvements seen in total annual catch and survey biomass for cod and flounder.

An exception was the survey index of cod abundance-at-age, which displayed a poorer fit in the expanded model. Of the stomach-content objective function components, flounder in Period 3 and halibut for all periods displayed the poorest fits. Sea lion indices most often incurred penalties in the objective function for exceeding the maximum acceptable limit for feeding on cod ages 4 – 8, and for sea lions aged 1 – 5 feeding on ages 5 – 10 pollock.

Estimated abundances for pollock and flounder increased in the expanded model (Fig. 1.1). These increases were generally most pronounced for younger ages and declined closer to core model values over time, although total estimated abundance remained greater for all years. Trends for cod abundance were less clear. Total estimated abundance was greater than the core model early on but fell below it in later years; the increase was primarily for ages 2 – 6 (Fig. 1.1). Selectivity curves differed from those assumed in the core model (Fig 1.2). Full-recruitment fishing mortality F followed trends similar to the abundances in Fig. 1.1 (not shown).

Halibut preyed primarily on pollock ages 2-5, but shifted the heaviest predation from ages 2 - 3 in early model years to ages 1 and 2 over time (Fig 1.3). Halibut predation on flounder occurred mainly from 1991 - 2001, and was concentrated on ages 2-5 (Fig 1.3). The lack of predation on flounder in early model years was due to the fact that no halibut stomachs were sampled prior to 1990.

Sea lions consumed predominantly mid-sized pollock ages 5 – 7 and cod ages 5 – 10 (Fig. 1.3). Predation mortality, distinct from stomach contents as it is affected by relative abundances of predator and prey ages, was highest for oldest pollock ages, while

predation mortality for cod was highest for ages 6 and 7 (Fig 1.3). Sea lions fed upon flounder as well, focusing on the oldest ages, but this predation was extremely minor, with all predation mortality on flounder from sea lion measuring less than 1%. All predation from sea lions dropped over time due to the decline in sea lion abundance. Pollock constituted an average of 25.5% of sea lion stomach-content by weight, cod an average of 20.2%, other food 53.9%, and flounder less than 1%. Younger sea lions fed more heavily on pollock (71.9% of diet by weight for age 1 sea lions), while older sea lions decreased their consumption of pollock (13.1% for age 13) and switched to cod (23.7%) and non-modeled prey (62.6%).

The addition of halibut and sea lions increased pollock total predation mortality for ages 2 – 5 and also for ages 8 – 10 (Fig. 1.4). Predation mortality on flounder declined, especially for early years and older ages, although the increased mortality from halibut predation on ages 2 – 5 was visible (Fig. 1.4). Cod exhibited large changes from core model trends, including a general reduction in prey linkages (Fig. 1.5), decreased predation on flounder, and a shift towards younger prey ages. These changes increased the relative proportion of M_0 to total mortality for flounder (Fig. 1.6), while the proportions for cod and pollock (Fig. 1.7) were roughly comparable between models.

DISCUSSION

Hollowed et al. (2000) constructed a predation model for pollock in the Gulf of Alaska in which the modeled predators were Pacific halibut, Steller sea lions, and

arrowtooth flounder. Predator abundances were set external to parameter estimation, and predation was estimated as a function of an age-dependent selectivity coefficient and a catchability term specific to each predator-prey combination. Modeled years ran from 1964 – 2002; predator diet data were taken from the REEM database from 1990 – 1996. In their model, sea lions consumed an average of 126.5 thousand metric tons (tmt) of pollock in 1997, halibut an average of 52.5 tmt and flounder 329 tmt. In contrast, the current work estimates total sea lion consumption of pollock in 1997 to be 50 tmt, total halibut consumption of pollock at 116 tmt, and total flounder consumption at 188 tmt. While estimates of pollock abundance were age structured, predator annual biomasses were aggregated over all predator ages into a single measure in Hollowed's work, which may account for some of the differences between studies. Hollowed's work also showed halibut selecting for older pollock, whereas the MSASA model placed the majority of halibut predation on pollock ages 2 – 5 and reduced halibut predation on pollock aged 6+. Both models displayed flounder preying on younger prey ages and placed flounder predation the highest of the three predator species in common.

The 2010 AFSC stock assessment for pollock in the GOA (Dorn et al. 2010) includes an ECOPATH (Christensen et al. 2000) model of pollock trophic dynamics based on REEM stomach-content data from 1990 – 1993, based on Aydin et al. (2007). Pollock were divided into juveniles (< 20 cm, corresponding to age 1 pollock in the current work), and adults (> 20 cm, corresponding to ages 2 – 10+). The top two sources of predation mortality for juvenile pollock were arrowtooth flounder (46.8% of total predation mortality) and adult pollock (11%); the GOA MSASA model showed the

highest predation mortality to come from adult pollock (56% of total predation mortality), followed by arrowtooth flounder (33.8%). For non-juvenile pollock (> 20 cm), the ECOPATH model showed the top pollock predators to be arrowtooth flounder (32.8%), Pacific halibut (22.9%), Pacific cod (16.2%), and Steller sea lions (6.2%). The MSASA model also placed arrowtooth flounder at the top of the list (45.4%) but listed Pacific cod as second (30.6%), followed by Pacific halibut (12.6%), and Steller sea lions (11.1%). (It should be noted that the relative proportions of predation mortality are not strictly comparable between the two approaches, as the ECOPATH model includes a number of other predators beyond those in the MSASA model.)

The GOA MSASA model differs significantly from the studies discussed above by the magnitude of pollock cannibalism shown in model outputs. While pollock cannibalism is a large trophic pathway in the Bering Sea, Yang (1993) found that this accounted for only 2.5% by stomach weight in the 1990 bottom trawl survey in the GOA. Hollowed et al. (2000) therefore did not include cannibalism as a potential predation vector. Dorn et al. (2010) showed cannibalism on age 1 pollock, but to a smaller degree than the GOA MSASA model.

The preference for mid-sized prey on the part of sea lions is supported by Trites and Calkins (2008), who found mean size of pollock consumed by sea lions to be 46 cm for males, and 39.8 cm for females (ages 3 -5 in the current work). This is somewhat different from Merrick and Calkins (1996), who found that for sea lions less than four years of age, 51% of the pollock consumed were under 30 cm (ages one and two), while 79% of the pollock consumed by adults were over 30 cm; the MSASA model showed all

ages of sea lions feeding more heavily on fish larger than 30 cm. It is also in contrast to Frost and Lowry (1986), who found mean size of sea lion prey to correspond to age 2 pollock, regardless of predator age, a finding mirrored in the eastern Bering Sea in the mid-1990s by Calkins (1998) and a literature review by Etnier and Fowler (2005). The use of minimum/maximum limits for estimated sea lion stomach-contents appears to be the best course of action given the disparities in the literature. The large influence of sea lion predation on predator-prey connections, however, requires improvements in sea lion diet assessment to adequately model such important system dynamics.

Predation mortality changes the structure of a population through the effects of cohort-specific predation. These changes are reflected in the selectivity values that indicate relative cohort abundances based on survey catches. As catch and survey data are assumed to have the lowest uncertainty of the data used in model fitting, they are consequently assigned the highest weights in the objective function. Model fitting may improve catch and survey fits at the expense of predation mortality components, resulting in erroneous deductions about predation functions, and model performance is highly sensitive to different model assumptions and approaches to data weighting.

Reduced uncertainty in diet data will improve model performance. Scarcity of diet information could potentially be augmented through analyses of stable isotopes and fatty acids to improve estimates of general feeding habits, but the drawback is that such work provides no information regarding prey age, which is integral to the MSASA structure. Predation models estimate increased prey biomass relative to single-species models (Kinzey and Punt 2009, Moustahfid et al. 2009). In an age-structured framework, M_0 is

raised when that increased recruitment is not completely removed due to predation but is instead passed through the population. In this context, M_0 for species subject to heavy predation is less a realistic indicator of a physiological mortality and more an indicator of the uncertainty contained within the modeled population that has yet to be explicitly defined (i.e. predators that were not included in the model). M_0 for pollock did not change from the core model because the additional predation was relatively evenly distributed over all age-classes by the new predators (Fig. 1.7); reductions in predation on younger ages from cod and flounder were replaced by predation from halibut, and remaining increased biomass in older ages was removed by sea lion predation. Conversely, predation on older flounder by cod was drastically reduced (Figs. 1.5 and 1.6), focusing the majority of predation pressure on ages 1 – 5. The disparity between predation on flounder ages was responsible for the increase in the relative proportion of M_0 to total mortality Z for older ages, and the sharp drop in selectivity values for ages 6+ (Fig. 1.2).

If the asymptotic progression of pollock M_0 towards zero is considered an indication of a minimal realistic predation model, further work is needed, especially as food web work such as Gaichas et al. (2010) found pollock to be fully utilized by GOA predators. Early experiments with unbounded sea lion size-preference parameters produced heightened predation on older pollock and cod, reducing pollock M_0 to 0.05; this assumption should be revisited along with others regarding model structure and included predators. M_0 may be asymptotic not to zero, but to some other measure of mortality indicative of a minimal necessary complexity, and is most likely different for

apex species such as halibut compared with forage species such as pollock (Gaichas et al. 2010).

The MSASA structure is capable of displaying the complex population dynamics needed for fisheries management, utilizing easily accessible data. Such an approach is needed in stock assessments to improve estimates of cohort structure, develop predation-robust biological reference points, and assess the impact of commercial biomass removals. Resolution of parameter confounding can be found in more abundant stomach-content data, reducing the number of possible model solution states, as well as external analyses directed towards improved estimates of survey selectivity curves. Updating the model to include the most recent data will aid in this, as well as simulation work to evaluate the influence of data scarcity and model specification on parameter estimates. Implementing these improvements will be a significant step forward in preparing the GOA MSASA model for practical application to fisheries management.

ACKNOWLEDGMENTS

The authors would like to thank Pat Livingston (AFSC-NOAA) and two anonymous reviewers for their suggestions and critiques of this paper. We also would like to thank Jim Ianelli (AFSC-NOAA), who provided the initial single-species code structure upon which the GOA MSASA model was constructed, Geoff Lang (ASFC-NOAA) who extracted the relevant stomach-content data from the REEM database for

our use, and Timothy Frawley, (Alaska Department of Fish and Game) who wrote a series of SQL queries to prepare the stomach-content data for inclusion into the model.

This work was funded by the Pollock Conservation Cooperative Research Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the Center or the University of Alaska.

This publication is also the result of research sponsored by Alaska Sea Grant with funds provided by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-11, 14), and from the University of Alaska with funds appropriated from the State. This publication is also the result in part of research and education sponsored by the Cooperative Institute for Arctic Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA17RJ1224 with the University of Alaska.

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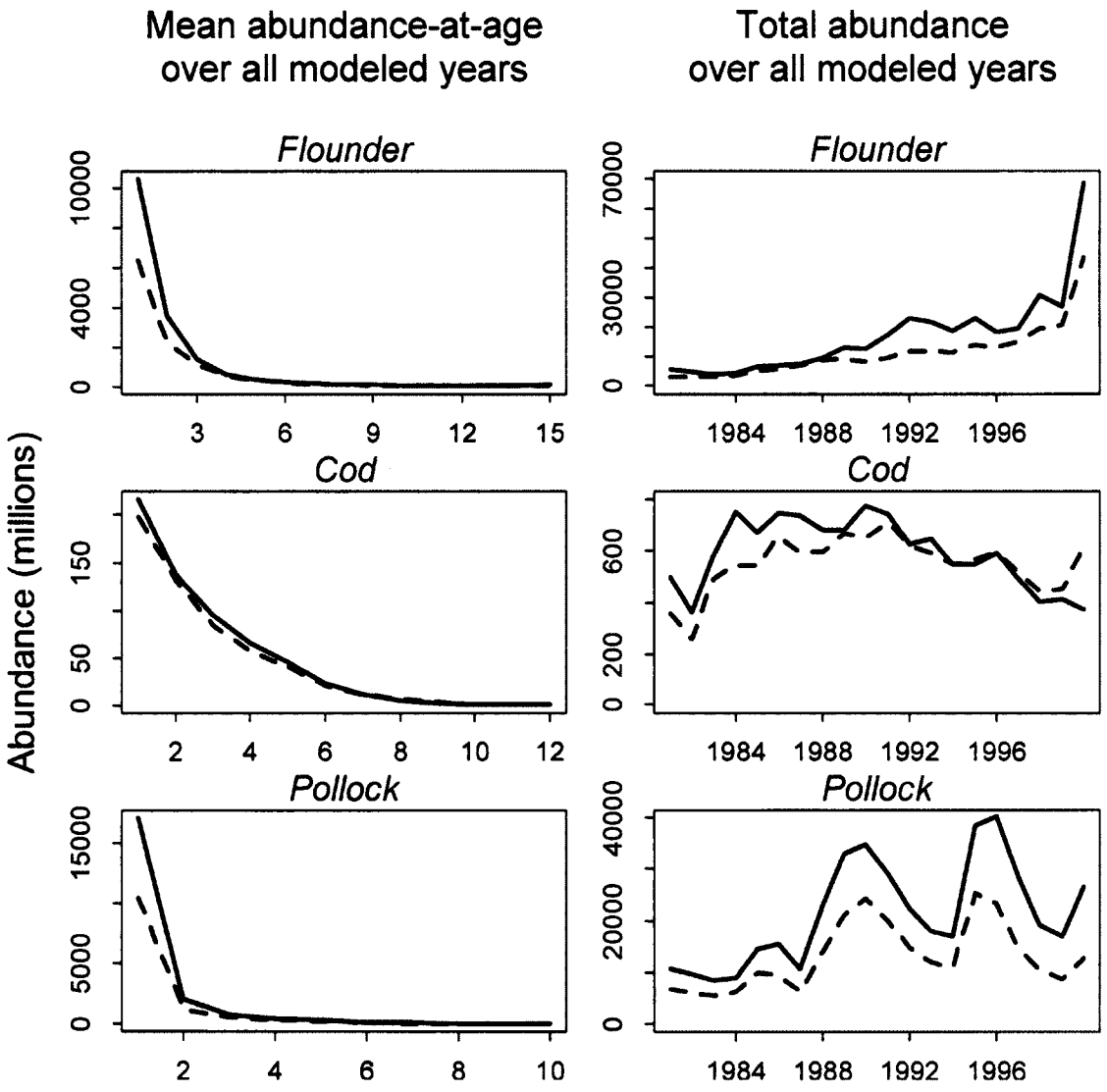

Figure 1.1. Changes in abundance from core model (dashed lines) to expanded model (solid lines).

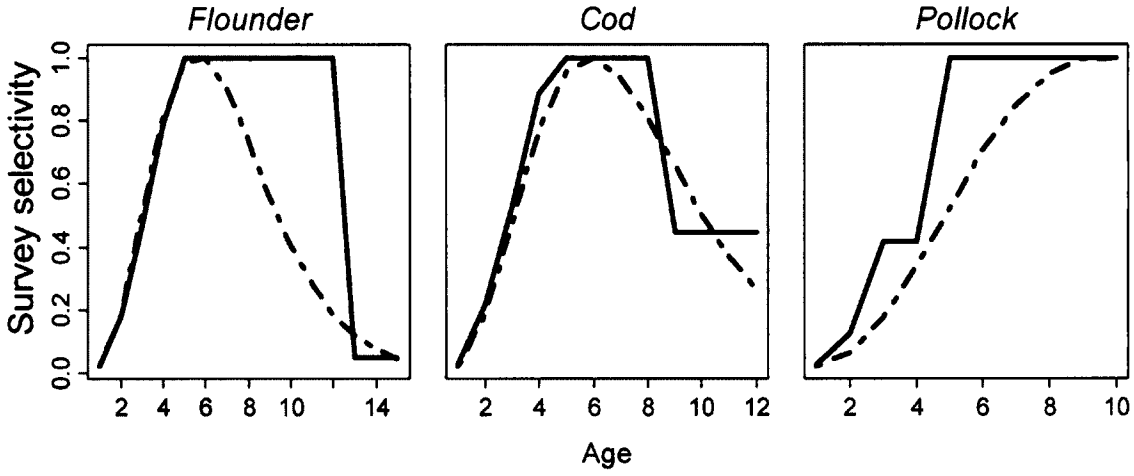

Figure 1.2. Changes to selectivity curves between core model (dashed lines) and expanded model (solid lines).

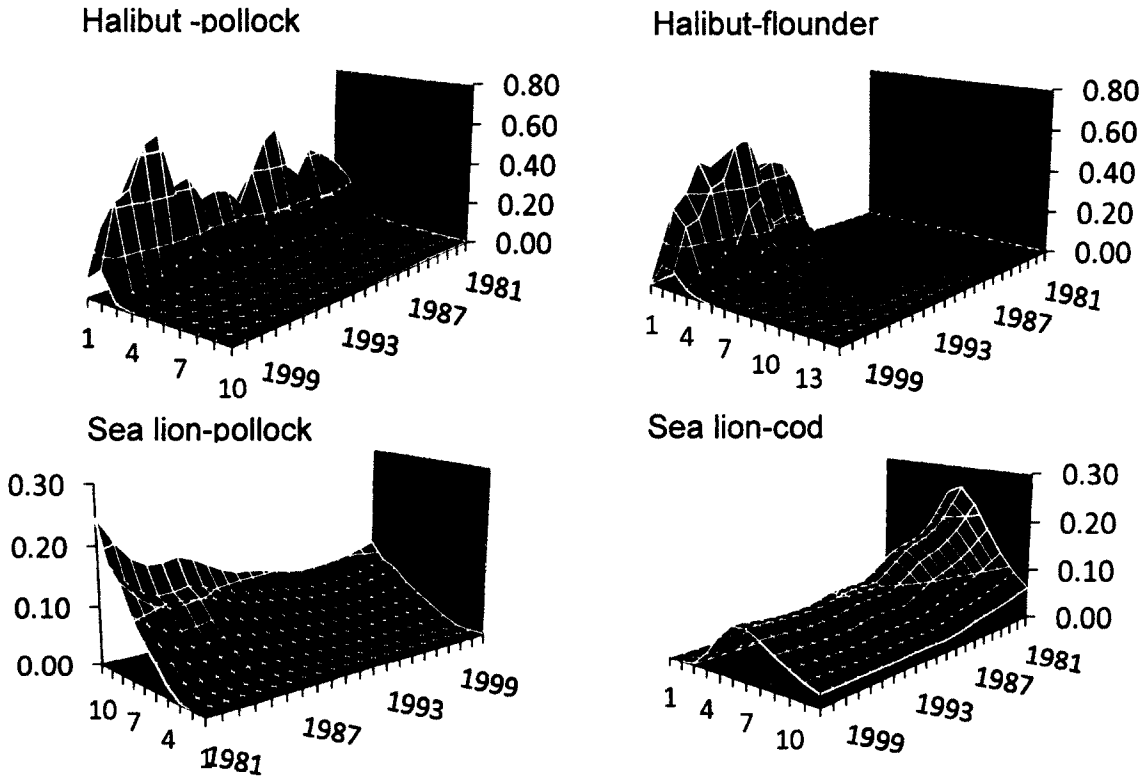

Figure 1.3. Predation mortality on pollock, flounder, and cod from halibut and sea lions, with age of prey on the x-axis, year on the y-axis, and mortality on the z-axis. Note reversed age-axis for sea lion preying upon pollock. Sea lion predation on flounder not shown.

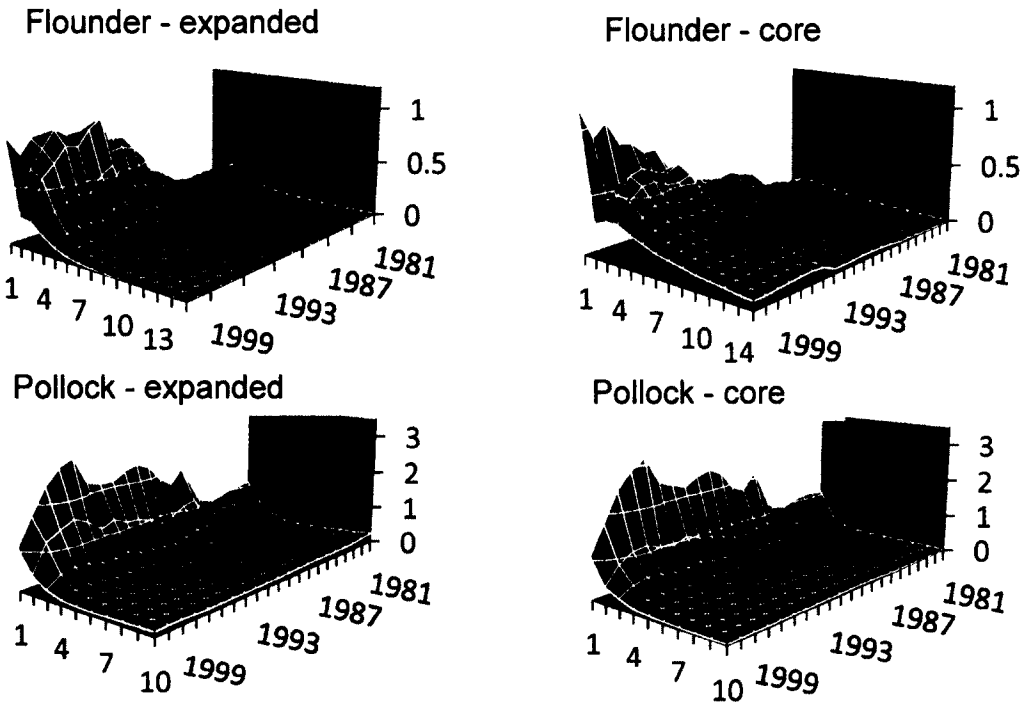

Figure 1.4. Total predation mortality on flounder and pollock from the core and expanded models, with age of prey on the x-axis, year on the y-axis, and mortality on the z-axis.

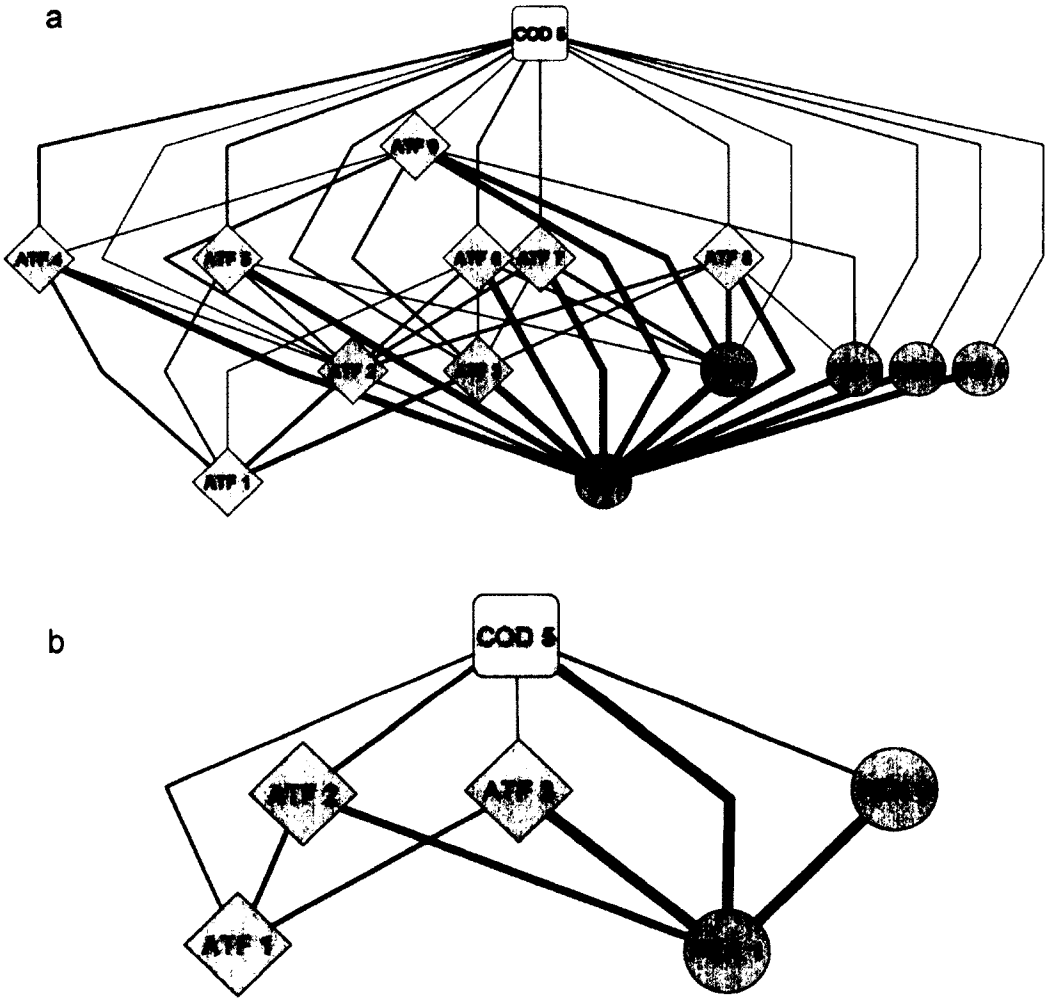

Figure 1.5. An example of changes in predation structure and trophic linkages for age 5 cod. Predation linkages from the core model (a) are simplified with a move towards smaller prey in the expanded model (b). Heavier lines indicate greater prey stomach-proportion by weight. Numbers refer to age. ATF = arrowtooth flounder, COD = Pacific cod, PCK = walleye pollock.

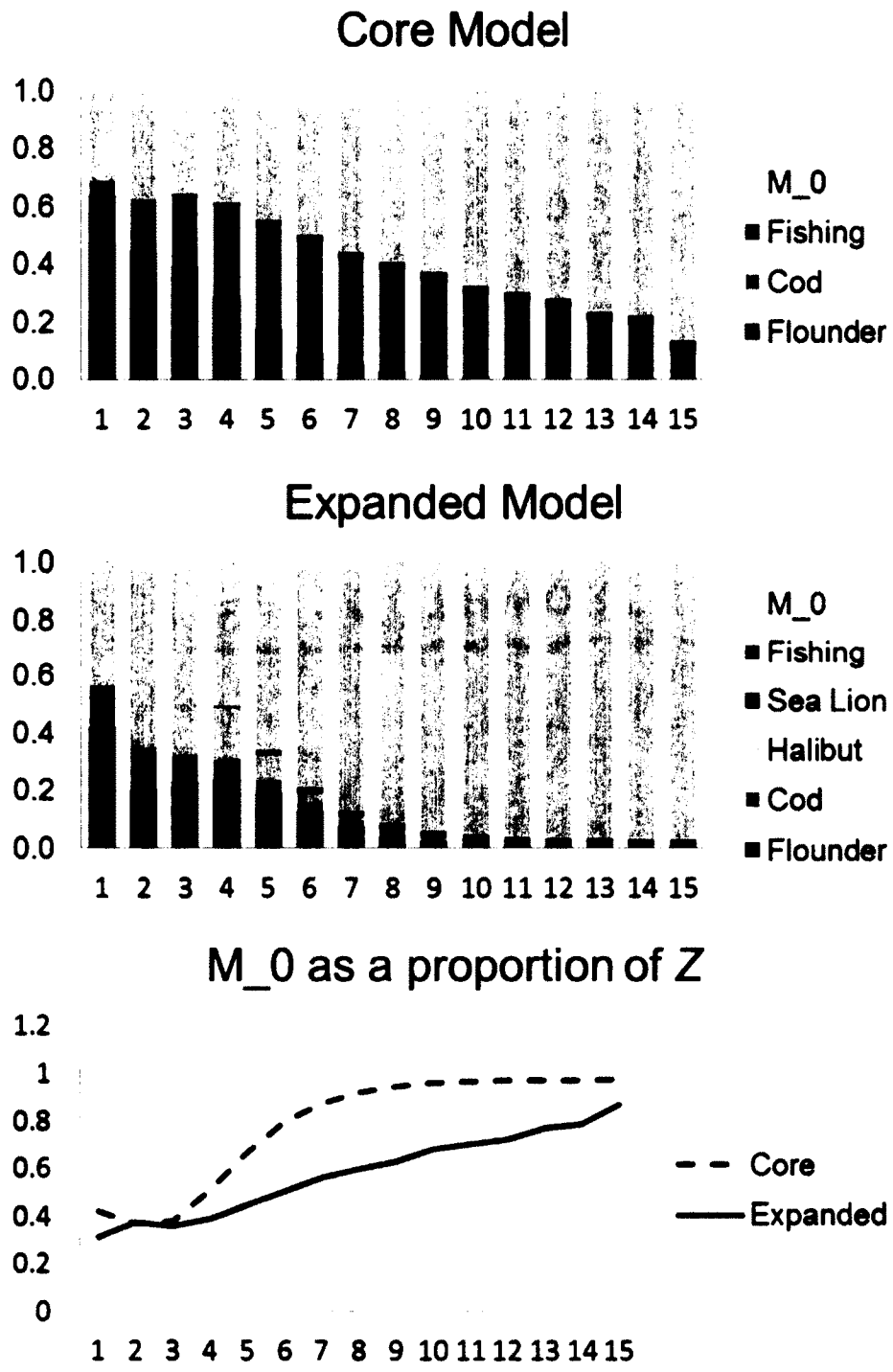

Figure 1.6. Components of total instantaneous mortality Z for arrowtooth flounder by age from the core model, the expanded model, and the difference between the relative contributions of M0 to Z between models. Values are averaged over all model years.

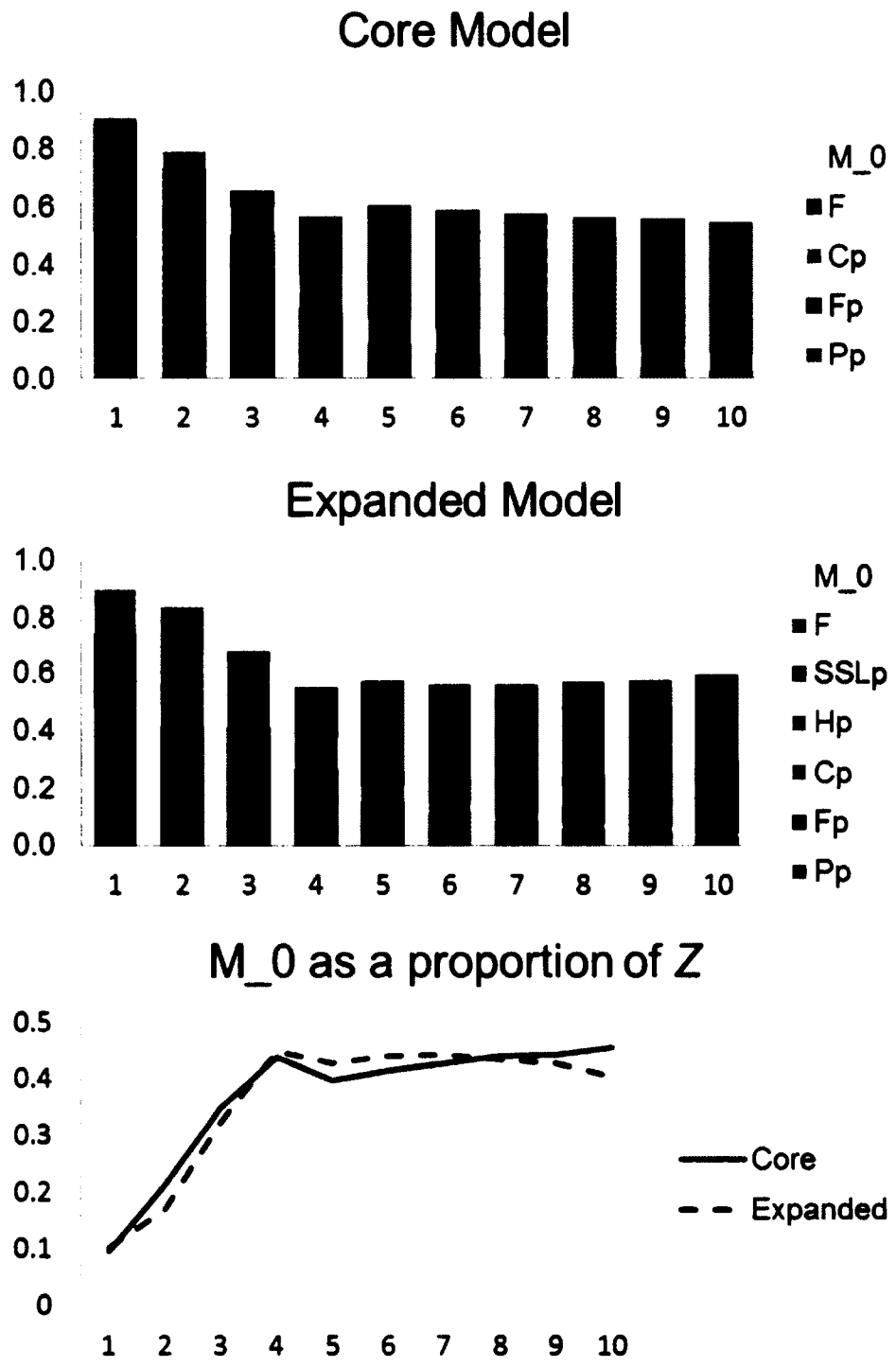

Figure 1.7. Components of total instantaneous mortality Z for walleye pollock by age from the core model, the expanded model, and the difference between the relative contributions of M0 to Z between models. Values are averaged over all model years.

CHAPTER 2

ASSESSING UNCERTAINTY IN A MULTISPECIES AGE-STRUCTURED ASSESSMENT FRAMEWORK: EFFECTS OF DATA LIMITATIONS AND MODEL ASSUMPTIONS[1]

[1] K.F. Van Kirk, T.J.Quinn II, J.S. Collie, and Z.T. A'mar. Assessing uncertainty in a multispecies age-structured assessment framework: effects of data limitations and model assumption. In preparation to be submitted to Natural Resource Modeling

ABSTRACT

Model performance and uncertainty in parameter estimation for a multispecies age-structured assessment (MSASA) model in the Gulf of Alaska (GOA) were examined through simulation exercises. Species included arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). Age-specific predation mortality was estimated as a flexible function of predator and prey abundances, fitted to stomach-content data. Simulated datasets were constructed by introducing random variability into estimates of catch, survey, and stomach contents from the operating model, whose structure was identical to that of the assessment model. Five simulation configurations were used to explore the effects of different levels of assumed data variability, mismatched assumptions regarding model structure, and lack of stomach-content data on model performance. Erroneous assumptions regarding model structure and lack of data had the greatest influence on parameter estimation bias and model performance. Integration of multispecies age structure into stock assessments can greatly reduce the bias arising from an assumed constant natural mortality and improve model realism, although the trade-off between realism and uncertainty must be evaluated prior to implementation.

KEYWORDS: multispecies, predation, Gulf of Alaska, walleye pollock, arrowtooth flounder, Pacific cod, stock assessment, Pacific halibut, Steller sea lion

INTRODUCTION

Age-structured modeling of fish populations uses information from a variety of data sources regarding mortality, recruitment, and other dynamics that may vary with age or size to create an assessment of the dynamics of the population of interest (Quinn and Deriso [1999]). Natural mortality, defined as all sources of mortality apart from those due to fisheries removals, is a key parameter in accurate fisheries modeling and stock assessment (Clark [1999], NRC [1998]). The majority of removals of a cohort for non-apex species is due to predation mortality (Gaichas et al. [2010], Andersen and Beyer [2006]), which can exceed removals from fishing mortality at older ages (Bax [1998]), affects abundance at all ages, and requires a multispecies approach when setting biological reference points for harvest control rules sensitive to population variability arising from predation (Tyrell et al. [2011], Collie and Gislason [2001]). Separation of predation mortality from other sources of natural mortality has been an on-going process; current models that distinguish predation from other natural mortality (e.g., Aydin et al. [2007]) are often used as adjunct sources of information about species interactions, but they are rarely directly integrated into stock assessments.

We developed a multispecies age-structured assessment (MSASA) model that extends a set of single-species age-structured models by linking them via predator-prey relationships (Van Kirk et al. [2012], [2010]). Designed to integrate predation into a statistical stock assessment framework, MSASA uses standard equations of single-species stock assessment models (Quinn and Deriso [1999]) to model year-class strength,

fishing mortality, survey indices and commercial catch, but decomposes total mortality Z into fishing mortality F, predation mortality P, and a residual natural mortality termed M_0. Predation mortality, estimated by age and year, is a flexible function of predator and prey abundances, estimated from size- and species-preference parameters in conjunction with annual ingestion requirements.

Catch, survey and stomach-content data were used for model fitting via maximum likelihood methods with AD Model Builder (Fournier et al. [2011]). By assuming that the stomach contents were sampled with error, MSASA allows the error associated with estimates of predation mortality to be quantified.

The MSASA model developed for the Gulf of Alaska (GOA) included walleye pollock (*Theragra chalcogramma*), arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumetopias jubatus*) (Fig. 2.1). Annual catches at age, survey abundances at age, fishing mortality, predation mortality, and a constant residual natural mortality term over years were estimated for pollock, cod, and flounder for 1981 through 2001. Steller sea lions and Pacific halibut functioned as predators only; their abundances were estimated externally and input for each year. Length and weight-at-age, fishery and survey gear selectivity, and annual predator ingestion rate were assumed to be constant over time. The exception was Pacific halibut, for which the annual weights-at-age, and therefore annual rations, changed each year. Catch and survey abundance data were taken from the Alaska Fisheries Science Center (AFSC) Stock Assessment and Fishery Evaluation (SAFE) reports, and stomach-content data for fish species were supplied by the Resource

Ecology and Ecosystem Modeling (REEM) database of the AFSC. A complete description of model structure and analyses of results is given in Van Kirk et al. ([2010], [2012]); model equations are presented in Appendix 2.

The purpose of this study is to evaluate the precision and accuracy of the GOA MSASA model through a series of Monte Carlo simulations in which the model is fitted to a variety of simulated datasets whose true means and distributions are known, and the resulting model performance assessed. We focus on ways in which model assumptions and data restrictions may affect estimates of predation and abundance. Including predation in stock assessment models may introduce significant uncertainty and instability into modeling efforts. Simulations attempt to quantify this uncertainty and examine the ways in which available data and assumptions can alter model output. Few evaluations of model performance have been undertaken (Curti, [2012]), but doing so is a necessity if these models are to be integrated into stock assessment efforts. These assessments become especially important when using such a model to analyze potential management strategies. Management actions in pursuit of a given goal lack an accurate assessment regarding their probability of success unless the range of uncertainty contained in the models used to generate them has been quantified (Punt [2006]).

METHODS

Simulation Structure

In the baseline scenario, the MSASA model functioned as both operating model (generating the simulated data sets) and assessment model, so that model misspecification and erroneous assumptions were avoided. This provided a benchmark for the evaluation of other scenarios in which deliberate model misspecification or data limitations were incorporated.

Five hundred simulated data sets were generated in the statistical programming language R (version 2.14.2) by the addition of random error to the point estimates of catch, survey and stomach-content data sets produced by the GOA MSASA operating model; the forms of these errors were drawn from the assumed underlying distributions of the AFSC and REEM data in the operating model (Table 2.1). Measurement errors for total annual catch and total annual survey abundance were drawn from lognormal deviations; errors in catch-at-age and survey numbers-at-age were simulated from a multinomial distribution with total assumed sample size $n = 100$ and assumed proportions-at-age. For stomach contents the current work departs from the methodology in Van Kirk et al. [2010, 2012]. Stomach contents were assumed root-normally distributed, for which the square root of the distribution was normal, with probability density function

$$\frac{1}{2\sigma\sqrt{x}\sqrt{2\pi}}\exp\left(-\frac{\left(\sqrt{x}-\mu\right)^2}{2\sigma^2}\right). \tag{2.1}$$

Using eq. (2.1) resolved issues with poor performance of random samples drawn from lognormal, multinomial, or normal distributions when attempting to construct simulated data sets for which many of the values were close to zero. The age-structured

maximum/minimum stomach-content bounds used for sea lion diet in earlier model configurations were discarded due to concerns over potential disproportionate influence on simulation results in the face of high uncertainty regarding bound values. Drawing on Aydin et al. [2007] and Trites and Calkin [2008], estimated sea lion predation was constrained such that the sum of each sea lion stomach produced general proportions by weight as: pollock = 0.4; cod = 0.15; flounder = 0.1 without any specifically defined age-structure of prey.

We simulated data from the operating model under five scenarios that differed in assumptions regarding data availability, data variability, and model structure:

SIM 1: This was the baseline scenario that used random draws for all key quantities generated by the operating model: catch-at-age, total annual commercial catch, survey-at-age, total survey biomass, and stomach contents for all ages of all predators. In contrast to the sometimes sparse stomach data available to the operating GOA MSASA model, SIM 1 contained stomach values for every potential combination of predator and prey species and age. The simulated stomach content data had therefore a greater influence on parameter estimates than actual stomach data used in the GOA MSASA operating model due to a larger number of data points in the objective function. It was expected that the results from this simulation would contain no bias and low variance.

SIM 2: In this scenario, random variation was introduced solely into the stomach-contents to examine the influence of error only in the stomach content data on overall parameter estimates; values for catch and survey indices were assumed known without error and set to the assumed true values (the point estimates from the operating model).

SIM 3: The variances of the random error distributions used to generate the simulated data sets were doubled from their original values to examine the influence of data variation on model performance; objective function weights remained unchanged. Here the estimation model underspecifies the uncertainty in all data quantities.

SIM 4: This scenario had the same number of stomach-content data points as did the operating model, thereby examining the influence of sparse stomach data on model performance (Fig. 2.2). Stomach-data were re-scaled so that the same amount of food was consumed by each predator as in SIM I. Stomach-content bounds for sea lions, however, did not change in this simulation.

SIM 5: This scenario examined the effects of deliberate misspecification of the assumed survey selectivity curves. This simulation replaced the operating model's double-logistic survey selectivity curves with non-parametric curves that were used in earlier stages of MSASA model development. These non-parametric curves were used to develop the initial three-species model that included flounder, cod, and pollock, but were replaced during the addition of halibut and sea lions when they became problematic to model convergence and parameter estimation. The approximation estimated selectivities for younger ages (for cod and pollock, ages 1 -4; for flounder, ages 1 – 5), set selectivities to 1 for middle ages (flounder: ages 6 – 12; cod: ages 5 – 9; pollock: ages 5 – 8), and estimated selectivity for older ages with a single coefficient for each species (flounder: ages 13 – 15; cod: ages 10 – 12; pollock: ages 9 – 10) (Fig. 2.3). All other aspects of the SIM 1 simulation structure remained unchanged. Selectivity for all other simulations was estimated, but the functional form was unchanged from the operating model.

All weightings in the objective function of each simulation were kept at the same values as the operating model to maintain consistency.

Evaluating Simulation Performance

The primary statistic to evaluate simulation performance in regard to bias was the distribution of relative errors, summarized by the median relative error (MRE), and defined as

$$\text{MRE} = median\left(\frac{\hat{\theta} - \theta}{\theta}\right) \tag{2.2}$$

for which $\hat{\theta}$ is the parameter value estimated by a given simulation and θ is the true value from the operating model. MRE is a measure of relative bias (the tendency of a simulation configuration to consistently over- or under-estimate parameter values). Wilcoxon/Mann-Whitley (W/MW) tests were also used to evaluate estimates of age-1 abundance and M_0 from each model against the operating model as well as each other.

The primary statistic to evaluate simulation performance in regard to precision was the coefficient of variation (CV). AD Model Builder (ADMB; version 10.1) uses finite difference approximation of second-order derivatives to calculate the asymptotic parameter variance-covariance matrices. For each scenario, the distribution of these variance estimates across all replicates was compared to the CV calculated from point estimates across replicates. Replicates for which ADMB was unable to generate variance-covariance matrices due to non-convergence were discarded.

For illustration, model performance was assessed by comparing the bias and CV statistics for estimates of residual natural mortality M_0, annual age-1 mean abundance, and total annual biomass for arrowtooth flounder, Pacific cod, and walleye pollock. Age-specific abundances and predation mortality were examined graphically.

RESULTS

General Population Structures

SIM 4 (modified stomach) had the largest number of replicates rejected due to non-convergence, requiring 981 total runs to produce the target 500 solution sets (Table 2.2). SIM 5 (model misspecification) had no rejected replicates, followed by SIM 2 (stomach only), with 589 total runs, SIM 1 (baseline) with 684 total runs, and then SIM 3 (variance doubled) with 726 total runs.

Wilcoxon/Mann values for SIM1 confirmed no bias only for median estimates of age-1 flounder abundance; all other estimates of age-1 abundance and M_0 were significantly biased relative to operating model values (Fig. 2.4). For both parameters, bias was consistently negative, with SIM1 underestimating both recruitment and residual natural mortality. Magnitude of bias was largest for pollock M_0, for which the maximum relative error over all replicates was -97%; bias was smallest for cod M_0 with a maximum relative error of -26%. Coefficients of variation (CVs) calculated from replicates of

parameter estimates were higher than median asymptotically-determined CVs for flounder and pollock, but slightly lower for cod (Fig. 2.5).

As with SIM 1, median estimates of age-1 abundance and M_0 in SIM 2 were all significantly biased relative to true values (Fig. 2.4), but deviated from SIM 1 results in that age-1 flounder displayed positive bias. Distributions of relative error narrowed relative to SIM 1 for estimates of age-1 abundance for all species and for cod M_0, but only slightly for flounder and pollock M_0. Distributions of asymptotic variances were also narrower than in SIM 1, except for pollock M_0, for which the distribution was slightly wider (Fig. 2.5). CVs for SIM 2 were also generally equal to or lower than CVs from SIM 1 (Fig. 2.5).

SIM 3 matched SIM 1 results in that median estimates of recruitment and residual natural mortality were significantly biased relative to true values. Median bias for flounder recruitment was positive as in SIM 2, and increased relative to SIM 2 from 5.7% to 21.5% (Fig. 2.4). Distributions of relative error were also wider in SIM 3 than SIM 1 or SIM 2 (Fig. 2.4), as were distributions of asymptotic variances (Fig. 2.5). CVs were higher than in SIM 1 or SIM 2.

Bias in SIM 4 estimates of recruitment and M_0 was significant as in SIM 1. Contrary to the results from SIM 1 – 3, bias was positive for flounder and pollock M_0 and negative for flounder abundance at age-1 (Fig. 2.4). Flounder M_0 had a maximum relative error over all replicates of 340%, larger than any other simulation. Median bias for pollock M_0 in SIM 1 – 3 ranged between -45% and -80%, but in SIM 4 shifted markedly to +26% (Fig. 2.4). Distribution of asymptotic variances and point estimates of CVs were

similar to SIM 1, with two exceptions: median asymptotic variance and the point estimate of CV for age-1 flounder in SIM 4 were higher than in other simulations, in addition to the distributions being wider (Fig. 2.5), and the variance of pollock M_0 dropped to virtually zero (Fig. 2.5).

Results for estimates of recruitment and M_0 in SIM 5 were similar to SIM 1 in that all bias was negative and statistically significant (Fig. 2.4). Median parameter values and relative error distributions were similar although not identical to SIM 1 results with the exception of estimates of age-1 recruitment and M_0 for pollock, which had greater negative bias and narrower distributions (Fig. 2.4). The greatest departure from SIM 1 results for CVs was for pollock M_0, for which the asymptotically-determined CV was larger than in any other simulation for either parameter, and for which the CV from the point estimate was higher (Fig. 2.5).

When W/MW tests were used to compare the results of each simulation to the others, median estimates of age-1 abundance and M_0 for cod in SIM 1 and SIM 3 were not significantly different from each other, and neither were median estimates of flounder M_0 for SIM 1, SIM 2, and SIM 3. All other median estimates of age-1 abundance and M_0 for all species between all simulations were significantly biased relative to each other (not shown).

Abundance-at-age trends for all species were very similar between simulations, with SIM 3 showing slightly higher variability than SIM 2, and flounder in SIM 4 diverging from the trends of other simulations (Fig. 2.6). Abundance-at-age generally displayed a negative bias except for age-1 flounder. Bias trends for cod and pollock were

similar, with the highest negative bias for youngest ages and the smallest bias for the oldest cohorts, and these trends appeared inversely correlated with trends in flounder bias, except in SIM 4. Pollock estimates were very similar across simulations, with highest bias in SIM 5. Cod displayed the least difference between simulations. Contrary to expectations, age-classes that were the focus of the heaviest predation exhibited no consistently greater width of relative error distribution than any other.

Total annual abundances for all three species (Fig. 2.7) showed expected differences between SIMs 1, 2, and 3, with the lowest error distributions for SIM 2 and the widest for SIM 3, while overall species-specific trends did not differ greatly between those simulations. SIM 4 and 5 showed low bias and narrow error distributions for cod. Pollock abundance varied more between years in SIM 4 than other simulations, and was underestimated with low variability for all years in SIM 5. While flounder abundance in SIM 4 also displayed higher inter-annual variability that in other simulations, the distribution of relative errors in SIM 5 was wider than all other simulations except SIM 3.

Median survey selectivity values for the SIM 1, SIM 2, SIM 3, and SIM 4 were virtually identical and matched true values closely (survey selectivity for the SIM 5 was input and not comparable). Median estimates of fishery selectivity differed little between simulations (not shown).

Predation Components

Estimates of fish predation-at-age were similar between SIM 1, SIM 2, and SIM 3 (Figs. 2.8 – 2.9). Predation on pollock by halibut and cod was overestimated, especially for younger ages (Fig. 2.8a, 2.8b), while predation on pollock from flounder was closer to operating model values except for age-1 (Fig. 2.8c). Predation on flounder from fish predators in SIM 1, SIM 2, and SIM 3 showed less bias than predation on pollock (Fig. 2.9a, 2.9b, 2.9c).

SIM 4 altered predation in a variety of ways due to the thinned stomach-content data. Halibut and cod predation on pollock were closer to operating model values than all other simulations, with the exception of younger ages, for which predation was increased (Fig. 2.8a, 2.8b). Flounder predation on all ages of pollock dropped (Fig. 2.8c). Reduced predation resulted in higher estimates of pollock M_0 (Fig. 2.4). Predation on flounder from all fish predators was reduced (Fig. 2.9a, 2.9b, 2.9c), and predation was generally shifted to younger ages of prey. Cod predation on flounder dropped to almost zero in SIM 4 (Fig. 2.9b). The decline in predation on flounder and flounder cannibalism resulted in a lower estimate of age-1 flounder abundance (Fig. 2.4) and a higher estimate of flounder M_0 (Fig. 2.4). As estimated flounder abundances were reduced due to shifts in stomach-content data, estimated flounder predation on pollock in SIM 4 (Fig. 2.8c) was the result of reduced flounder abundance and not a direct consequence of the thinned stomach-content data as flounder species-preference coefficients changed little (Fig. 2.11), and flounder stomach contents were similar to operating model levels (Fig. 2.12).

Predation on pollock from halibut and cod was highest in SIM 5, especially for younger ages (Fig. 2.8a, 2.8b), while predation on pollock from flounder was unbiased (Fig. 2.8c). Predation on flounder from fish species was comparable to operating model values and SIM 1, 2, and 3 (Fig. 2.9b, 2.9c), with the exception of halibut preying on younger flounder, for which predation increased (Fig. 2.9a)

Sea lion predation on pollock (Fig. 2.10a) and flounder (Fig. 2.10c) in SIMs 1 – 3 was overestimated at oldest ages, and was highest on pollock in SIM 5, while the highest levels of predation on flounder were from SIM 4. Sea lion predation on cod (Fig. 2.10b) differed somewhat from operating model values, but matched general trends.

Species-preference coefficients were virtually identical for SIM 1 – 3, differing slightly in SIM 4 and 5 (Fig. 2.11). Coefficients from the operating model were somewhat different from all simulation estimates, with the exception of flounder in SIM 1 – 3 (Fig. 2.11).

Stomach contents were similar between the operating model and all simulations except SIM 4 (Figs. 2.12 – 2.14). Size-preference curves also differed only in SIM 4, in which flounder (Fig. 2.12), cod (Fig. 2.13) and halibut (Fig. 2.14) shifted towards selection of smaller prey relative to the operating model and other simulations. Sea lion size-preference curves were slightly narrower for all simulations relative to the operating model, but did not otherwise differ (not shown).

DISCUSSION

The fact that SIM 2 displayed predation trends and parameter estimates similar to SIM 1 and SIM 3 strongly suggests that uncertainty in diet data is a major influence on model bias and precision. As cod had only a single predator whose abundances were input, variability in predation mortality-at-age was lower than for pollock and flounder and contributed less to overall variability in parameter estimates, which is why distributions of relative error were narrowed more in SIM 2 for cod than for the other prey species. It was expected that SIM 2 would display much lower variances than were observed, especially for pollock and flounder, and it may be that changes in model performance were somewhat constrained by the fact that the relative variance between different data sources remained constant for all simulations.

Uncertainty in stomach data (SIM 4) had the greatest effects on estimation precision and accuracy of the GOA MSASA model, followed by errors in model specification (SIM 5). This was expected, but the mechanisms by which model performance is influenced are intricate in models this complex.

Thinning the simulated stomach-content data sets in SIM 4 reflected the higher frequency with which younger pollock and flounder prey were present in the REEM samples, relative to less likely instances of predation on older prey (Figs. 2.12 – 2.14). While the size-preference curves shifted slightly in response to this, it appeared that the pollock prey items remaining in the simulated data sets were sufficient to drive the estimation of the size-preference coefficients such that the resulting estimated stomach

contents in SIM 4 were close to the true values from the operating model despite the loss of prey data. The reduction in estimated predation on flounder from fish predators (Fig. 2.9a – c) was the result of the shift towards smaller prey along with lowered species-preference coefficients targeting flounder (Fig. 2.11). The increase in the estimated sea lion preference for flounder (Fig. 2.11) and predation on flounder (Fig. 2.9d) worked in conjunction with reduced flounder recruitment and increased M_0 to bring estimates of flounder abundances closer to operating model values.

Predation on ages 1 - 3 pollock in SIM 4 was higher for halibut and cod than in the operating model (Fig. 2.8a – b), but close to true values for older ages; bias for estimates of abundance-at-age for those older ages was therefore lower in SIM 4 than other simulations. The fact that pollock M_0 in the SIM 4 had a positive bias strongly implied that the increase in M_0 was necessary to compensate for reduced predation on pollock ages 4 - 10.

SIM 5 contained erroneous assumptions about age selectivity that produced inaccurate estimates of predation, but the effects of these assumptions on model accuracy were less than the reduced stomach data in SIM 4 and less than expected. The most significant deviations from operating model selectivities were for flounder age 7 – 12, which were assumed to be 1 in SIM 5 but were markedly less than 1 in the operating model (Fig. 2.3). By overestimating survey selectivity for ages 7 – 14, SIM 5 underestimated flounder abundance more than other simulations (Fig. 2.6). Estimates of flounder recruitment and residual natural mortality, however, were similar to other simulations except for SIM 4, and the slightly lower estimation of flounder abundance for

ages 1 – 6 relative to SIM 1 – 3 was the product of increased halibut predation on ages 2 - 6 as opposed to reduced flounder recruitment.

Curti [2012] constructed a statistical age-structured multispecies model of the Georges Bank fish community. Monte Carlo simulations, incorporating error into simulated data sets for catch, survey, and stomach-contents, found results similar to this study, including bias in simulation estimates of age-1 recruitment and age-1 predation mortality, and species-preference coefficients highly sensitive to the inclusion of error in the simulated data. Although the relative strength of predator-prey linkages remained uncertain, both studies found predation trends to remain robust to a variety of error assumptions. Given that SIM 1, SIM 2, and SIM 3 were similar in median parameter estimates and predation dynamics, the tendency of the MSASA structure to exhibit bias in estimates of age-1 abundance and M_0 (for example) is most likely a product of the model's core predation equation in Table 2.2 of the Appendix, in which predation mortality is estimated from abundances at the beginning of each modeled year, as opposed to mid-year or other sub-annual time-scale.

Curti [2012] found that estimates of predation mortality-at-age and age-1 recruitment were more sensitive to uncertainty in survey data than in catch data. In this study, however, the size-preference curves in SIM 4 appeared to be successfully estimated with the thinned pollock stomach data. Thus, it is also possible that survey selectivity curves can aid in the estimation of size-preference, and, in turn, predation. In traditional single-species models, survey selectivity and natural mortality M, estimated as a free parameter, are confounded (Thompson [1994]). Including predation in population

dynamics, however, fundamentally changes the interaction between survey selectivity and mortality. The standard equation for survey numbers-at-age ns_a for a given species in a given year is

$$ns_a = s_a Q N_a \tag{2.3}$$

in which s_a = survey gear selectivity for age a, Q = survey catchability for the species under consideration, and N_a = total abundance at age a. Abundance-at-age can be defined in terms of recruitment and mortality as

$$N_a = N_1 e^{-\sum_{x=1}^{a-1} Z_x} \tag{2.4}$$

in which N_1 refers to recruitment at age-1, and $\sum_{x=1}^{a-1} Z_x$ is the sum of total mortality for all years 1 through a-1. For simplicity, let us assume an unfished population ($F = 0$), and that $Q = 1$. In that case, $Z = M$, and survey numbers-at-age can be written

$$ns_a = s_a N_1 e^{-\sum_{x=1}^{a-1} M_x}. \tag{2.5}$$

If it is correct that natural mortality M for non-apex species is composed entirely of predation P, then eq. (2.5) can be rewritten as

$$ns_a = s_a N_1 e^{-\sum_{x=1}^{a-1} P_x}, \tag{2.6}$$

and replacing P with the terms from the predation mortality-at-age equation (Table 2A.2, Appendix 2A) produces

$$ns_a = s_a N_1 e^{\sum_{x=1}^{a-1} \frac{1}{B_x} \sum_j \sum_b I_{j,b} N_{j,b} \frac{\phi_{x,j,b}}{\phi_{j,b}}}, \tag{2.7}$$

with the result that survey numbers-at-age are defined in terms of predator abundance and annual ration without recourse to a free parameter *M*. As the only sources of mortality are predation removals, annual reductions in cohort abundance are constrained by predator abundance, annual ration, and size/species-preference coefficients; cohort structure is indicated by survey numbers-at-age and created by predation mortality. The implication is that estimated survey numbers-at-age and predation mortality should work in conjunction to produce improved estimates of cohort structure and overall abundance. As survey components in the objective function carry a higher weighting than stomach-content data, survey data aid in the estimation of size-preference parameters. It should be noted that this is a result of a modeling approach only; in reality, many other factors affect survey abundance and whether they are incorporated into the model structure will affect the degree to which population assessments will be improved.

SIM 5 highlights the tradeoff between bias and variance when selecting an appropriate model structure. In this instance, SIM 5 often estimated lower parameter variances than the other configurations, but was the least accurate in its assessment of population structure and dynamics. The assumption of a fixed value of 1 for survey selectivity for various ages reduces overall model uncertainty by decreasing the number of model-estimated parameters, but model results are then dependent on the accuracy of such assumptions. This is especially true for the parameters which define survey selectivity, as survey selectivity plays a pivotal role in determining the cohort structure of a given population.

The fact that SIM 5 had a 100% convergence rate with no failures was counter-intuitive, given the earlier problems with convergence when using the SIM 5 selectivity curves. As predation mortality-at-age, M_0, and survey selectivity are confounded, it may be that by not estimating full-recruitment survey selectivities, this confounding was avoided, enabling a better convergence rate. It is also possible that the lack of explicitly-defined age structure in the sea lion stomach-content objective function components resulted in a greater flexibility in estimates of sea lion predation, allowing it to compensate for shifts in other predation parameters.

The weightings and assumed variances of datasets used in model fitting are important. These values have significant influence on estimates of model uncertainty and the relative influence of any given data set on parameter estimation (Deriso et. al. [2007]). Predation mortality-at-age is estimated as the ratio of biomass-at-age consumed to total biomass-at-age in a given year, meaning that low predator abundance and high prey abundance can present the same predation curve as high predator abundance and low prey abundance, provided that the linking parameters (species- and size-preference) and M_0 values can compensate accordingly. Moreover, the misspecification of predation linkages between species can produce biased predation estimates for one prey age while estimates for another age may be unbiased.

When fitting to observed stomach-content data, then, model "decisions" to modify predator abundances, prey abundances, size- and species-preference parameters, and/or M_0 to produce a given set of predicted stomach-contents should be constrained by fitting to catch and survey data sets first, for which the assumed variances are lower than for

stomach-content data and in turn serve as the primary repository of information regarding the abundance of adult populations (Francis [2011]). Radomski et al. [2005] found that potential errors in model specification could possibly be corrected by the incorporation of objective function weights and assumed data variances deliberately designed to allow for such flexibility. The fluidity in sea lion predation as a compensatory mechanism in SIM 4 and SIM 5 was an example of this flexibility, made possible by the use of the non-age-structured diet bounds, but also points out the sensitivity of model performance to assumptions regarding diet. A different weight on sea lion diet proportions would likely have altered model output, but the lack of informative age-structured data makes selection of an appropriate weight problematic.

Multiple sources of age-structured information (catch and survey data, stomach-content data) and multiple assumptions regarding cohort structure and species interactions can contribute to the accurate modeling of population structure. SIM 1 generated reasonable parameter estimates and matched operating model abundance and predation trends. SIM 2 demonstrated that error in predation information alone is sufficient to create uncertainty in population parameter estimates. SIM 3 showed that underestimating the variance of data increases model uncertainty, but this effect can be reduced provided that sample size is sufficiently large and that the assumed underlying distribution of each data source is complete and accurate.

Of the potential sources of uncertainty examined in the current work, errors in model specification and stochasticity in stomach-content data were the primary sources of degradation in MSASA model performance. SIM 5 affected the survey estimates that

are fundamental to model fitting, while SIM 4, following the example of SIM 2 in which variability in stomach-content data was sufficient to affect parameter estimation, degraded model performance even more than catch and survey fitting.

The effects of uncertainty in stomach-content data can potentially be reduced provided sufficient data are present for a given prey species to allow estimation of an accurate size-preference curve for the predator under consideration, even if other prey species are poorly represented in the sampled data. The complementary functions of survey selectivity and predation mortality may also help to constrain the effect of uncertainty and allow for changes in size-at-age where appropriate. Stock assessments are complex undertakings that direct significant time and energy to reducing errors in model specification. The increased uncertainty in parameter estimates from direct integration of age-structured predation mortality should be relatively minor and likely worth the improved realism from reduction of the bias incurred by the assumption of a constant natural mortality.

ACKNOWLEDGMENTS

This work was funded by the Pollock Conservation Cooperative Research Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the Center or the University of Alaska.

This publication is also the result of research sponsored by Alaska Sea Grant with funds provided by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-11, 14), and from the University of Alaska with funds appropriated from the State.

This publication is also the result in part of research and education sponsored by the Cooperative Institute for Arctic Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA17RJ1224 with the University of Alaska.

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Table 2.1. Operating model objective function weights and the associated variances used for random draws to construct simulated data sets.

Component	Distribution	Weight	Variance for random draws
Total annual catch	Lognormal	$1/\sigma^2$	Flounder: 0.141; Cod: 0.141; Pollock: 0.224
Total survey biomass	Lognormal	$1/\sigma^2$	Flounder: 0.119; Cod: 0.229; Pollock: 0.283
Catch-at-age	Multinomial	100	Effective sample size = 100
Survey-at-age	Multinomial	100	Effective sample size = 100
Stomach contents:			
Fish species:	Root normal	$1/\sigma^2$	0.224 for all species
Sea lions:	Root normal	$1/\sigma^2$	0.224

*Sea lions have no matrices of gut-content point estimates due to lack of stomach data. Estimated sea lion predation is conditioned such that the sum of each sea lion stomach will produce general proportions by weight as: pollock = 0.4; cod = 0.15; flounder = 0.1 without any specific age-structure of prey.

Table 2.2. Comparison of simulation convergence rates.

Simulation	Total runs to obtain 500 unique solution sets
S1 (base model)	684
S2 (stomach only)	589
S3 (variance doubled)	726
S4 (modified stomach)	981
S5 (model misspecification)	500

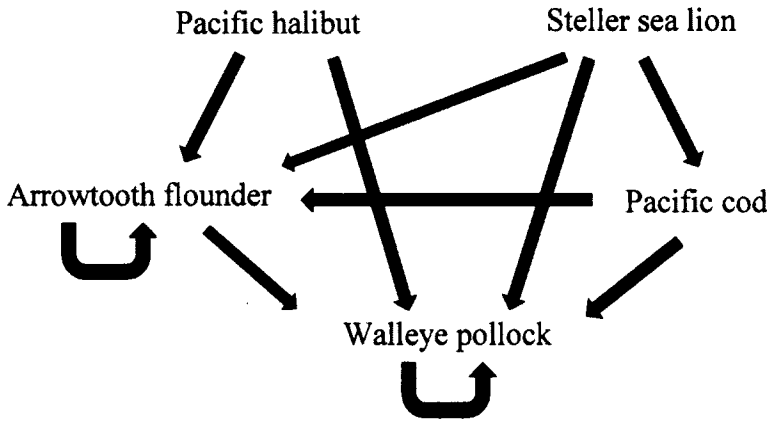

Figure 2.1. Predation linkages in the GOA MSASA model; curved arrows indicate cannibalism.

	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11	c12
p1	0.228	0.369	0.345	0.258	0.173	0.111	0.071	0.047	0.032	0.022	0.016	0.012
p2		0.038	0.080	0.107	0.114	0.107	0.093	0.078	0.066	0.055	0.047	0.041
p3			0.024	0.051	0.077	0.094	0.102	0.104	0.103	0.099	0.095	0.090
p4			0.009	0.023	0.041	0.058	0.071	0.079	0.083	0.086	0.087	0.086
p5			0.000	0.013	0.025	0.038	0.049	0.058	0.064	0.068	0.070	0.072
p6				0.007	0.014	0.023	0.031	0.037	0.042	0.046	0.049	0.050
p7				0.003	0.008	0.013	0.018	0.022	0.026	0.028	0.030	0.032
p8				0.002	0.004	0.007	0.010	0.013	0.015	0.017	0.018	0.020
p9				0.001	0.003	0.004	0.006	0.008	0.010	0.011	0.012	0.013
p10				0.000	0.004	0.006	0.010	0.013	0.015	0.018	0.020	0.021
OF	0.714	0.52	0.46	0.441	0.432	0.424	0.415	0.41	0.407	0.406	0.407	0.408

p1	0.286	0.480	0.540	0.300	0.225	0.128	0.099	0.065	0.045		0.048	
p2				0.124	0.149	0.122	0.129	0.109	0.094	0.093		
p3				0.059	0.100	0.108	0.142	0.145	0.147	0.166	0.285	0.216
p4				0.027	0.054	0.067	0.098	0.109	0.119	0.144	0.260	0.206
p5						0.044		0.080	0.091	0.114		0.170
p6						0.026	0.043	0.052	0.061	0.077		
p7												
p8									0.021			
p9									0.014			
p10												
OF	0.714	0.52	0.46	0.441	0.432	0.424	0.415	0.41	0.407	0.406	0.407	0.408

Figure 2.2. An example of the full complement of cod stomach-content data generated by the operating model utilized in SIM 1 (upper matrix) compared with the reduced stomach-content data utilized in SIM 4 (lower matrix) for which c1 – c12 = predator cod ages 1 – 12; p1 – p10 = prey pollock ages 1 – 10; OF = "Other Food" (non-modeled prey). Hatched cells define combinations of predator and prey ages that are removed from consideration by the size-preference function; empty cells in the lower matrix are combinations of predator-prey ages that can carry non-zero values but for which no information was present in the sampled stomach-content data.

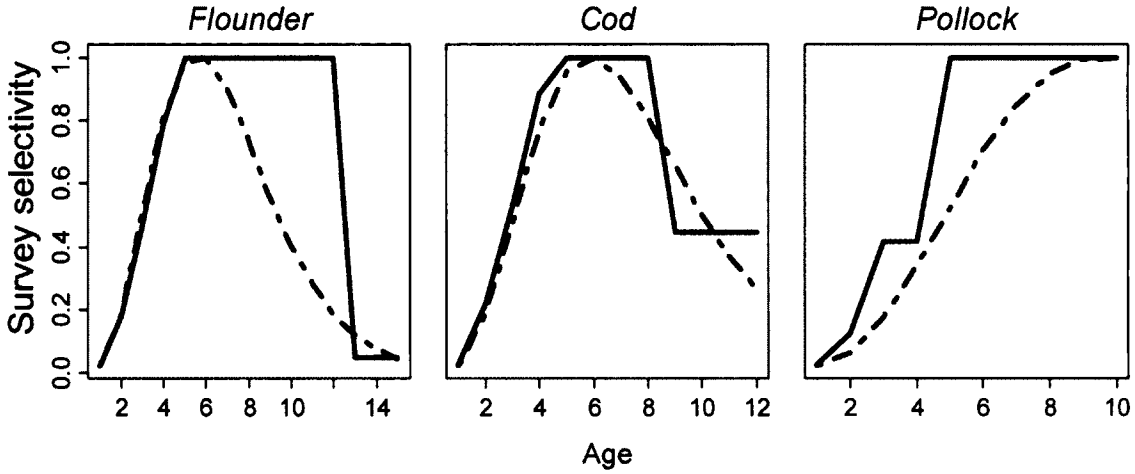

Figure 2.3. Changes to selectivity curves in SIM 5 (solid lines) relative to operating model curves (dashed lines).

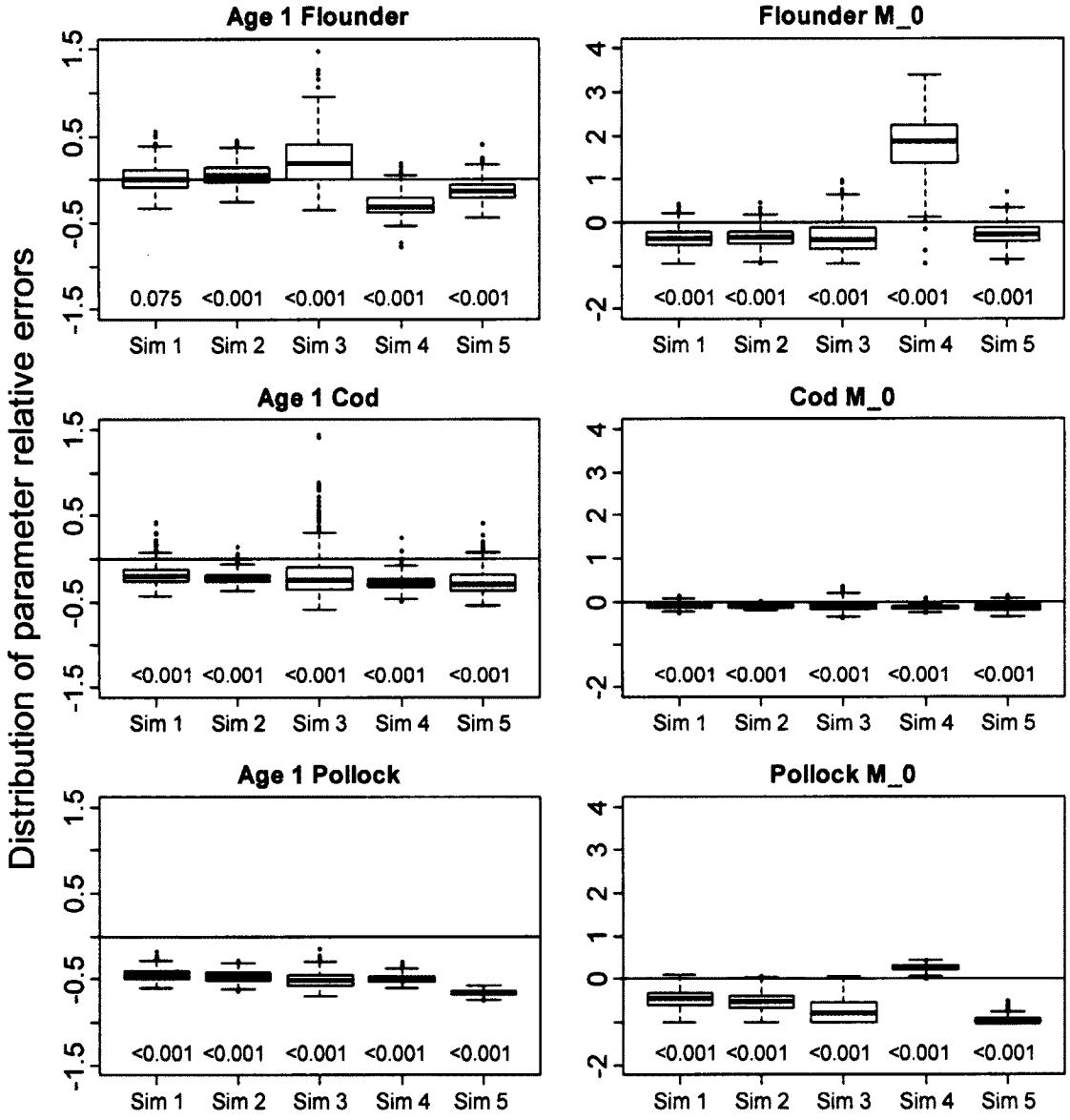

Figure 2.4. Distribution of parameter relative errors for age-1 mean abundance and residual natural mortality relative to operating model values for SIM 1 (base model), SIM 2 (stomach only), SIM 3 (variance doubled), SIM 4 (modified stomach), and SIM 5 (model misspecification). Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range. Wilcoxon/Mann *p*-values are given at the bottom of each plot describing the probability that the median parameter estimate is not significantly different from operating model values.

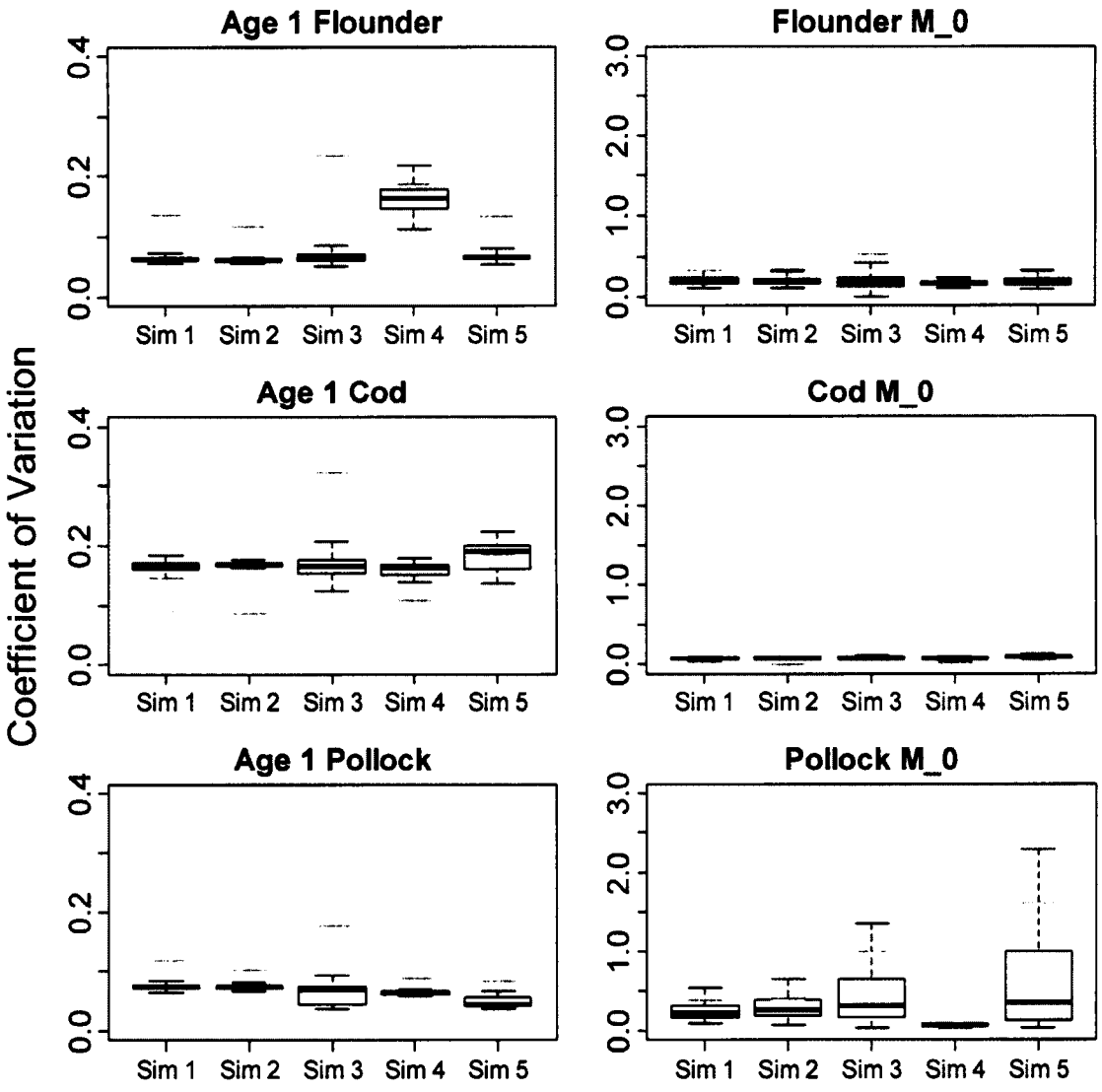

Figure 2.5. Boxplots of the distribution of asymptotically-determined coefficients of variation across replicates for each simulation compared with coefficients of variation calculated from point estimates (orange bars) for age-1 mean abundance and residual natural mortality for SIM 1 (base model), SIM 2 (stomach only), SIM 3 (variance doubled), SIM 4 (modified stomach), and SIM 5 (model misspecification). Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range.

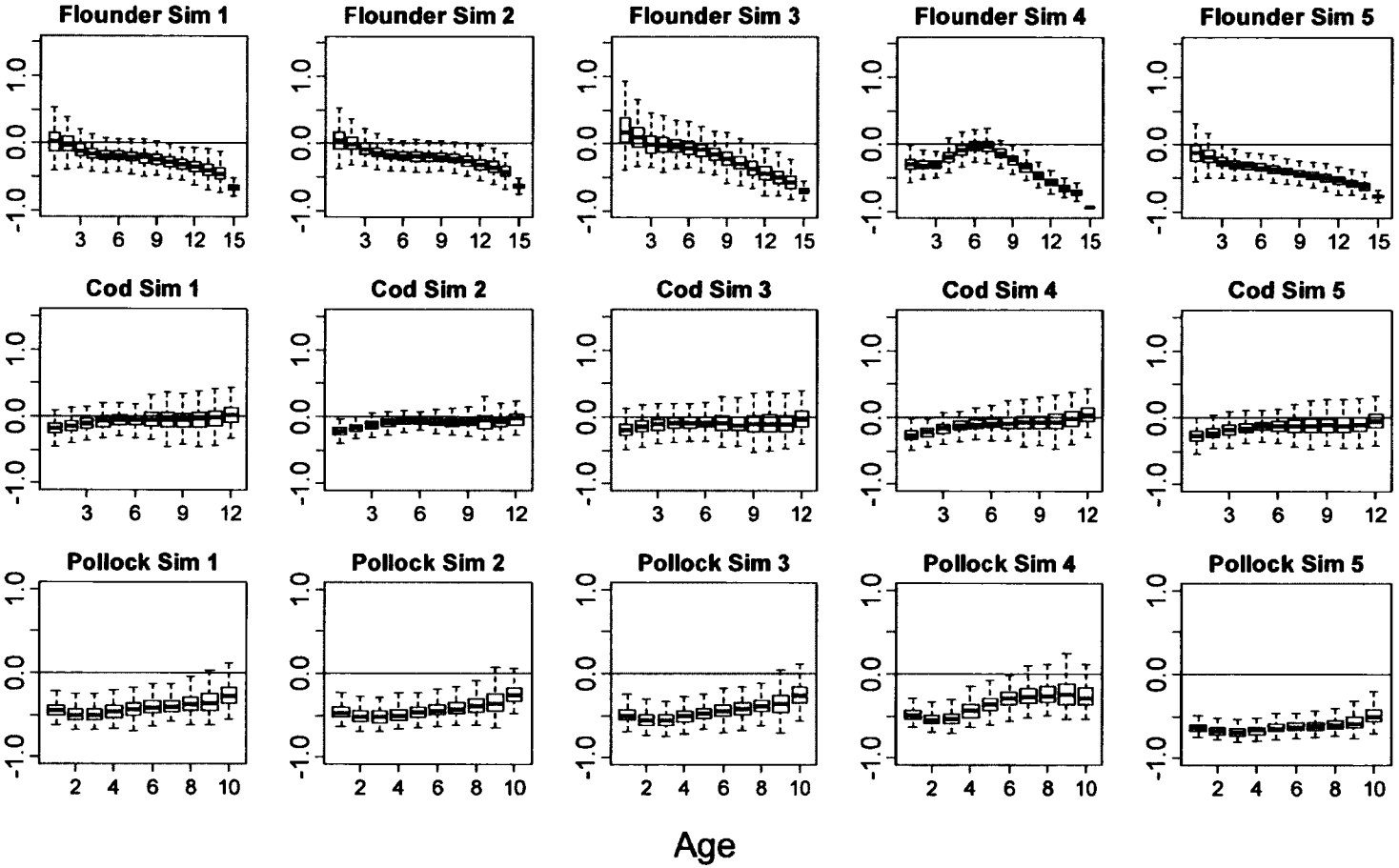

Figure 2.6. Distributions of relative error values for flounder, cod and pollock abundance-at-age for SIM 1 (base model), SIM 2 (stomach only), SIM 3 (variance doubled), SIM 4 (modified stomach), and SIM 5 (model misspecification) relative to operating model values. Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range.

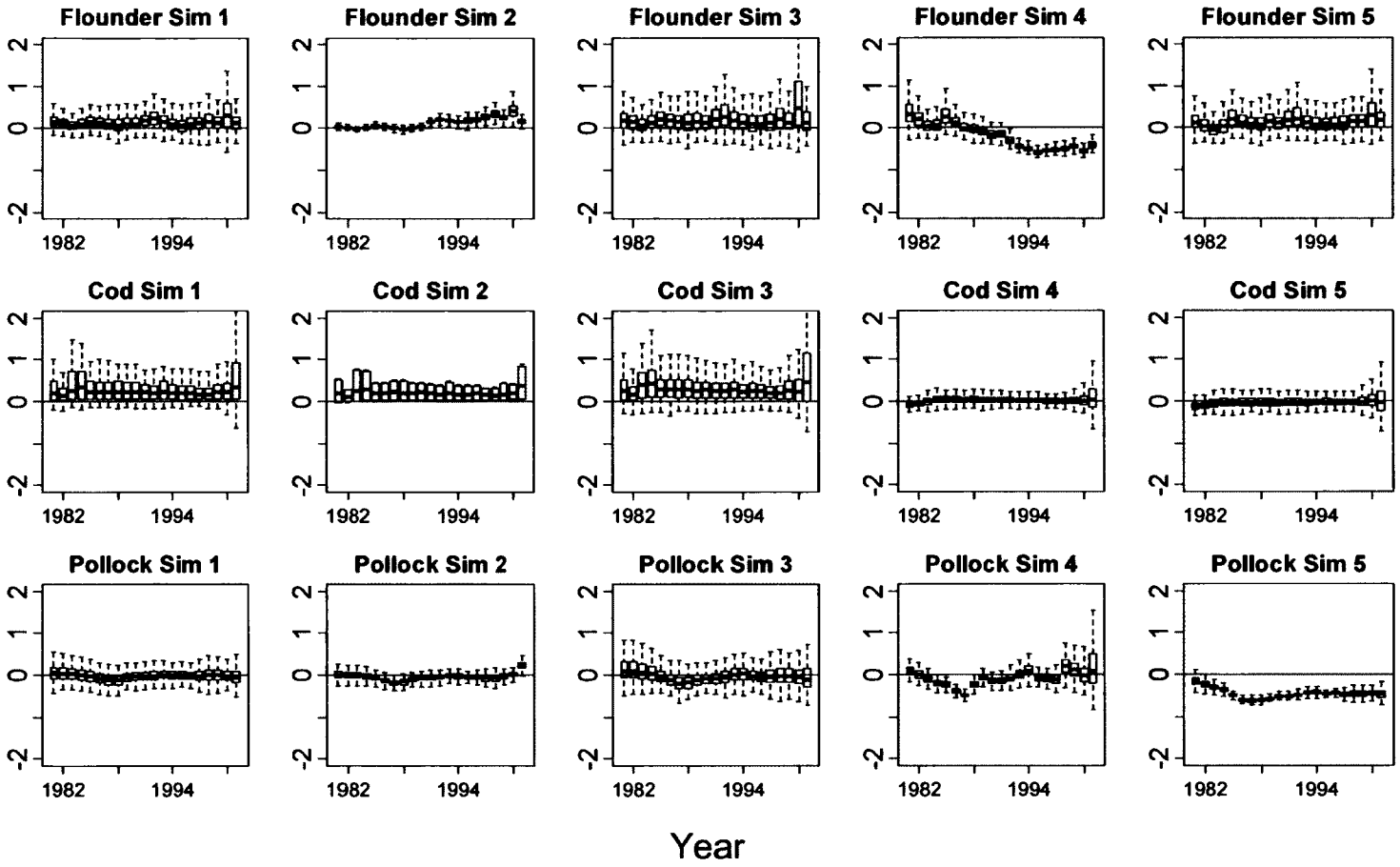

Figure 2.7. Distributions of relative error for flounder, cod and pollock total annual abundance for SIM 1 (base model), SIM 2 (stomach only), SIM 3 (doubled variance), SIM 4 (modified stomach), and SIM 5 (model misspecification). Boxes describe the interquartile range; vertical lines at ends of whiskers bounded by 1.5 times the interquartile range.

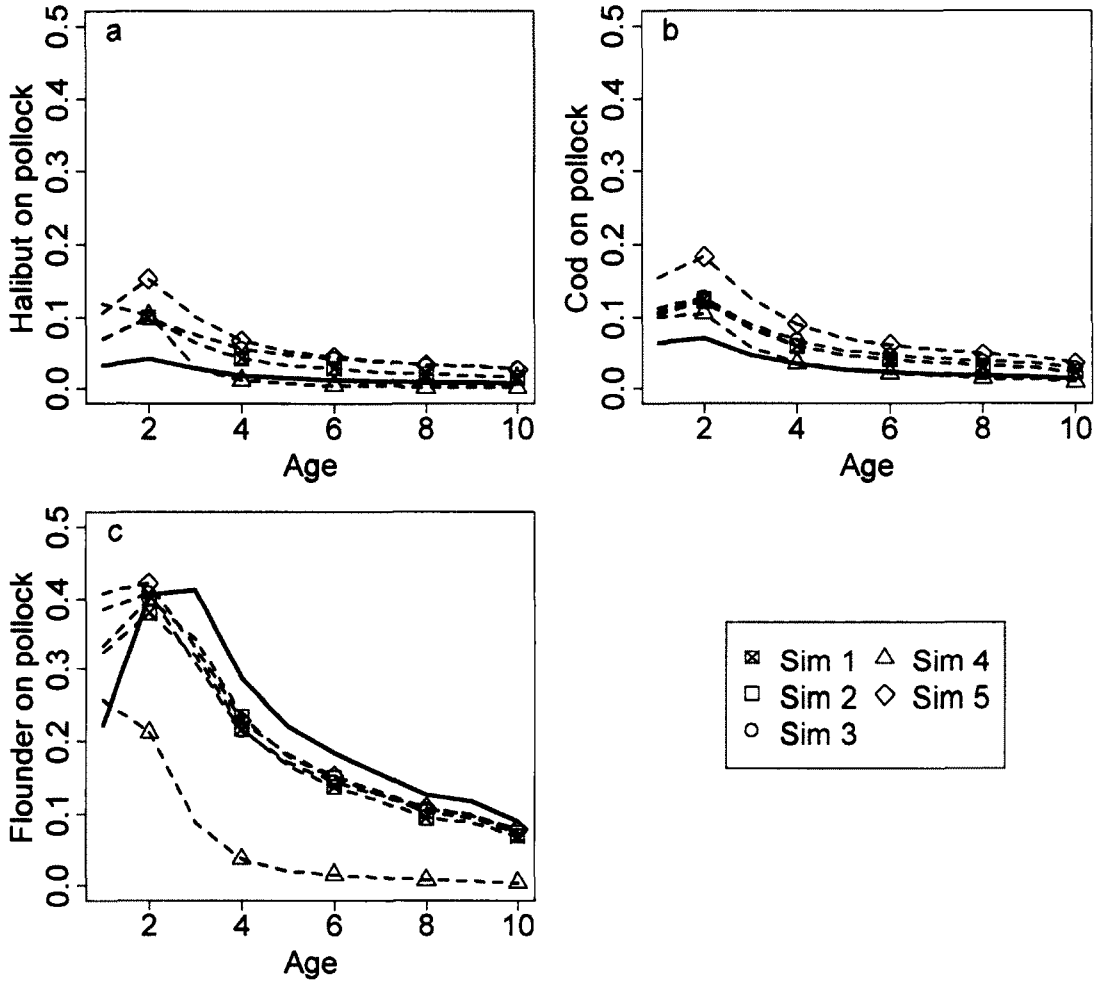

Figure 2.8. Median estimated predation-mortality-at-age for pollock from (a) halibut, (b) cod, (c) flounder for the operating model (solid line) and Sim 1 – 5 (legend).

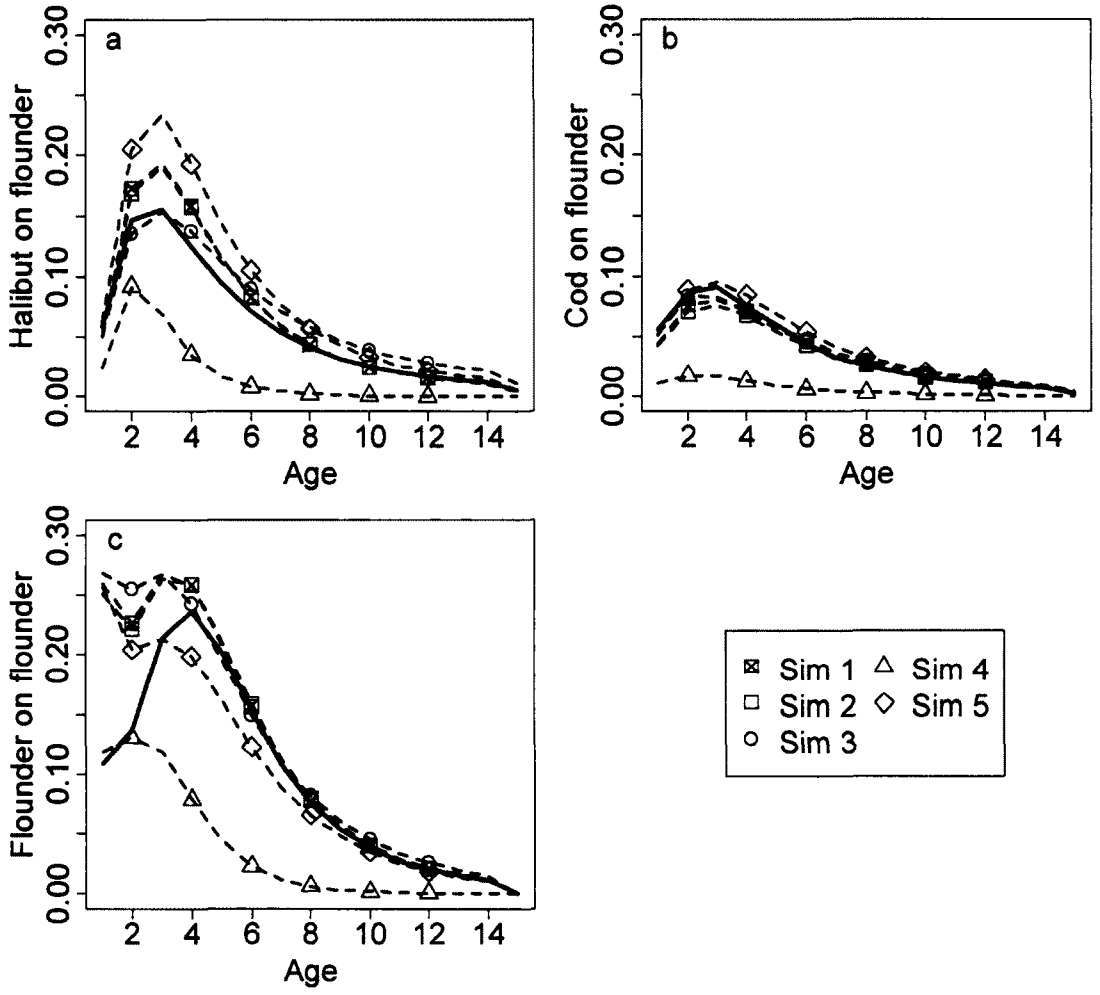

Figure 2.9. Median estimated predation-mortality-at-age for flounder from (a) halibut, (b) cod, (c) flounder for the operating model (solid line) and Sim 1 – 5 (legend).

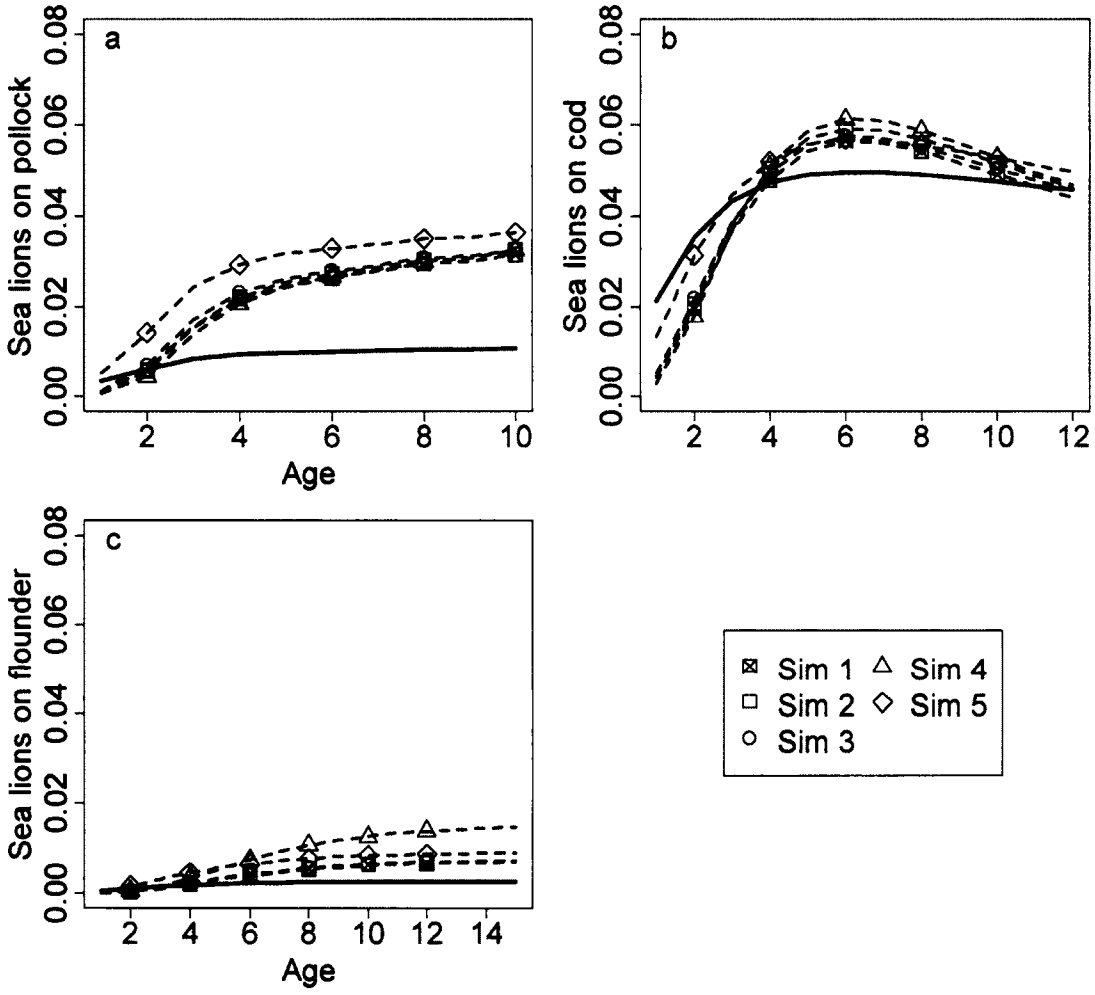

Figure 2.10. Median estimated predation-mortality-at-age from sea lions for (a) pollock, (b) cod, and (c) flounder for the operating model (solid line) and Sim 1 – 5 (legend).

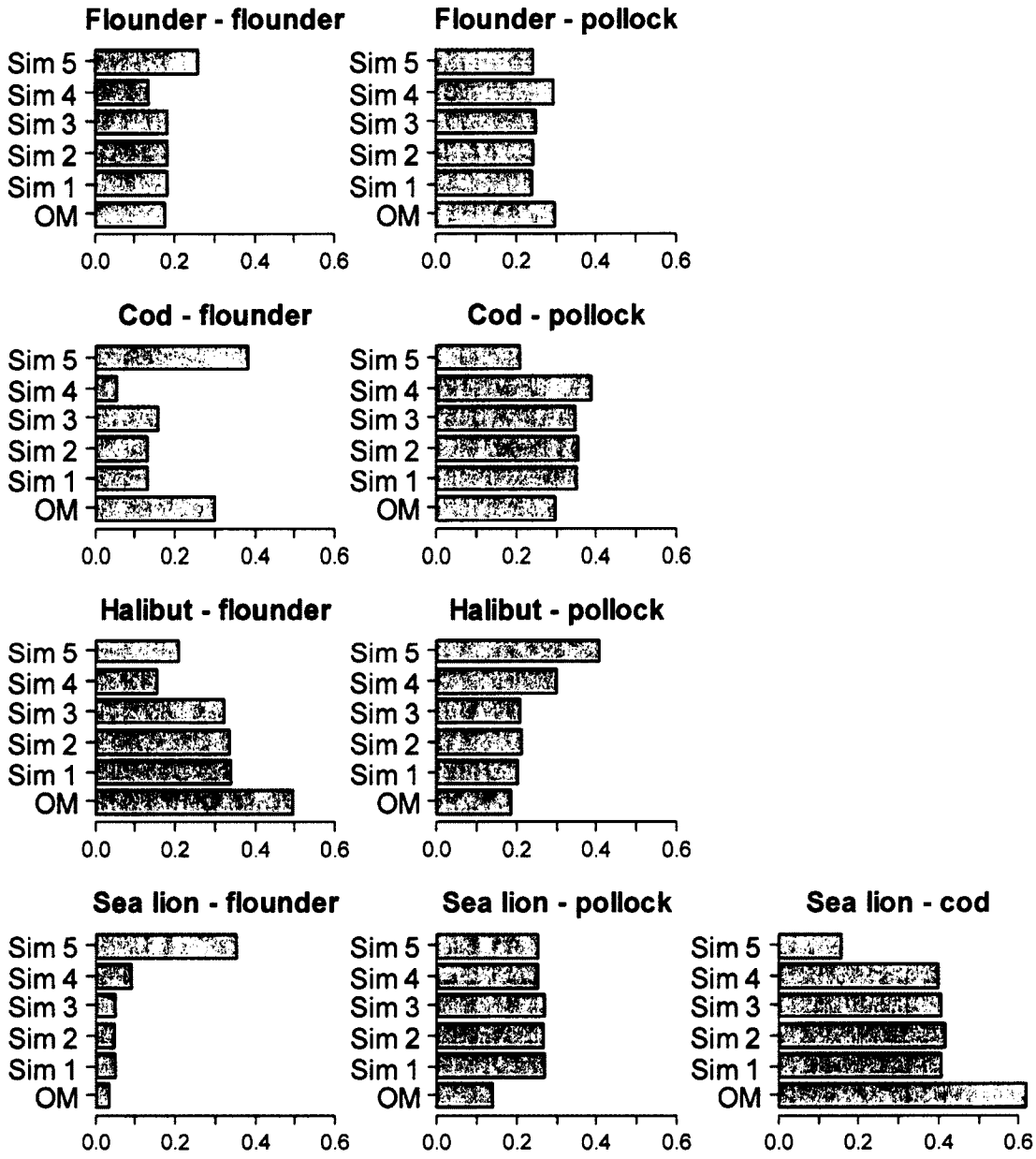

Figure 2.11. Median species-preference coefficients for flounder, halibut, cod, and sea lions from Sim 1 – 5.

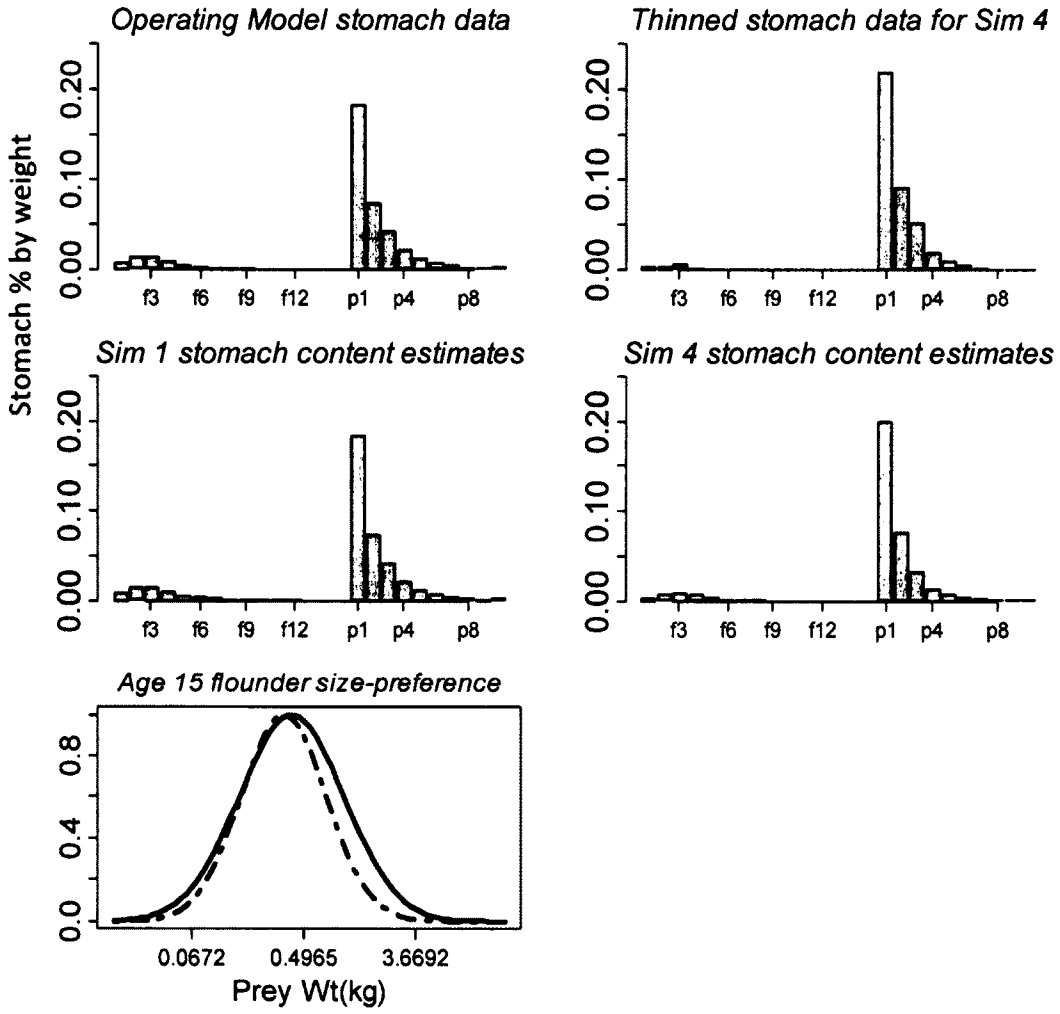

Figure 2.12. Median stomach-contents by proportion for flounder, averaged over all years and ages, and size-preference curves from SIM 1 (solid line) and SIM 4 (dashed line) for age 15 flounder. Stomach-contents and size-preference curves were sufficiently similar for SIM 1, 2, 3, and 5 that they are not shown for clarity. "Other Food" proportion in stomach not shown.

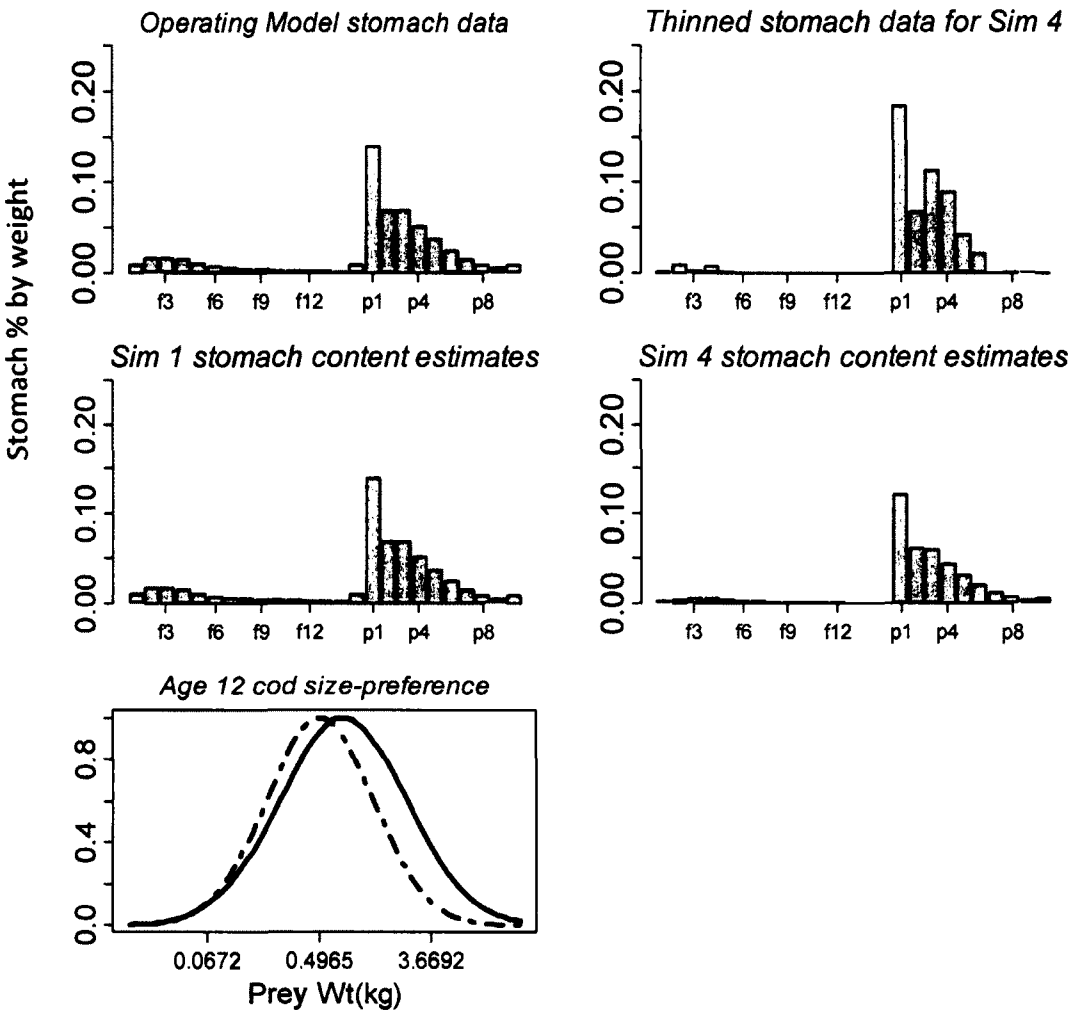

Figure 2.13. Median stomach-contents by proportion for cod, averaged over all years and ages, and size-preference curves from SIM 1 (solid line) and SIM 4 (dashed line) for age 12 cod. Stomach-contents and size-preference curves were sufficiently similar for SIM 1, 2, 3, and 5 that they are not shown for clarity. "Other Food" proportion in stomach not shown.

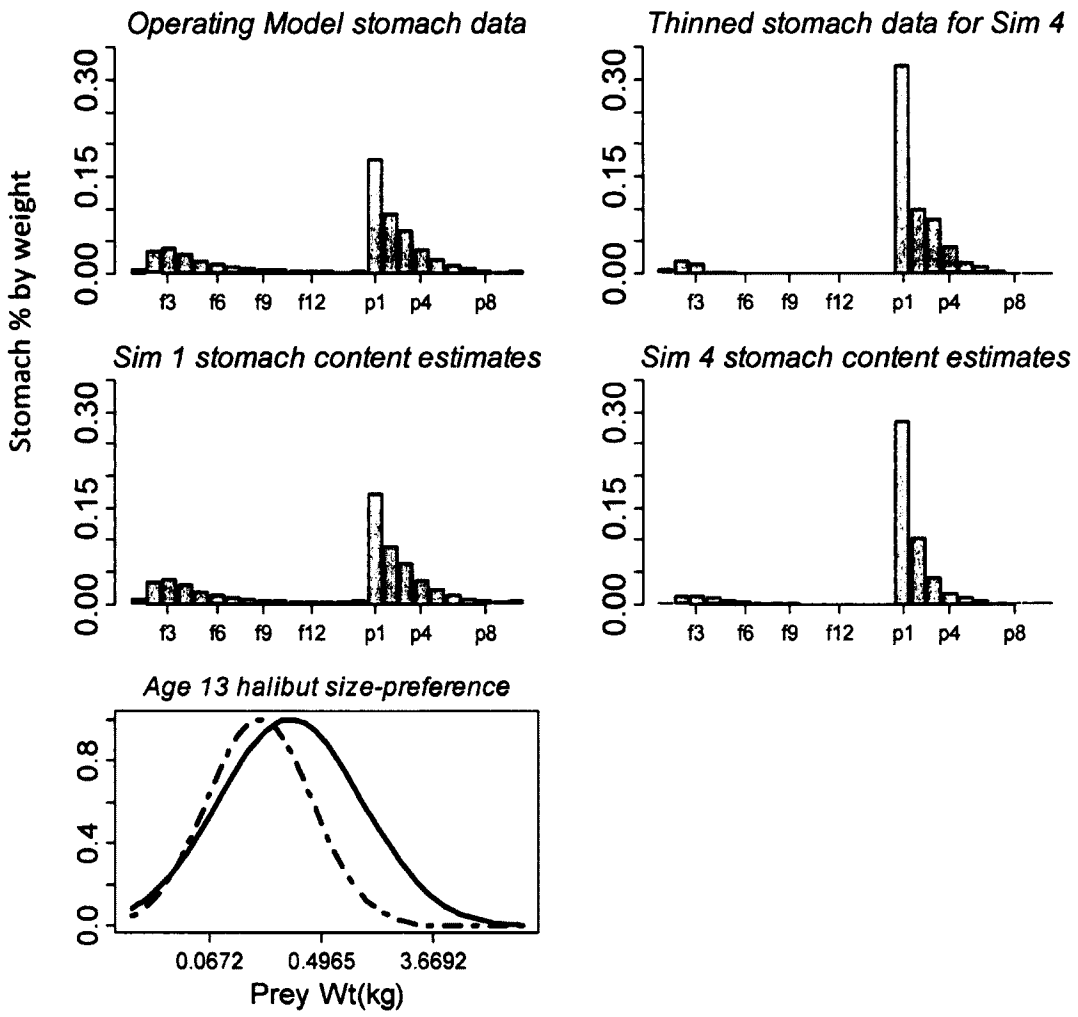

Figure 2.14. Median stomach-contents by proportion for halibut, averaged over all years and ages, and size-preference curves from SIM 1 (solid line) and SIM 4 (dashed line) for age 13 halibut. Stomach-contents and size-preference curves were sufficiently similar for SIM 1, 2, 3, and 5 that they are not shown for clarity. "Other Food" proportion in stomach not shown.

APPENDIX 2A
Data sets and equations for construction of the Gulf of Alaska multispecies age-structured assessment model and Monte Carlo simulations

Table 2A-1. Population dynamics equations as per Van Kirk et al. [2010] and Quinn and Deriso [1999].

Equation	Description
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}}$	Abundance of species i at age a+1 in year t+1 as a function of abundance at age a and year t.
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}} + N_{i,a+1,t}e^{-Z_{i,a+1,t}}$	Abundance of the plus group of species i at age $a+1$ in year t.
$F_{i,a,t} = s_{f_{i,a}}F_{i,t}$	Fishing mortality of species i at age a in year t.
$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}}e^{-Z_{i,a,t}}N_{i,a,t}.$	Commercial catch-at-age of species i at age a in year t.
$S_{i,a,t} = Q_i s_{s_{i,a}} N_{i,a,t}$	Survey abundance-at-age of species i at age a in year t.
$Z_{i,a,t} = F_{i,a,t} + P_{i,a,t} + M_{0_i}$	Total mortality-at-age Z, the sum of fishing mortality, predation mortality, and residual natural mortality M_0.
Q_i	Survey catchability for species i.
$s_{f_{i,a}}$	Fishery selectivity-at-age for species i at age a
$s_{s_{i,a}}$	Survey selectivity-at-age for species i at age a
$F_{i,t}$	Full-recruitment fishing mortality for species i in year t.

Table 2A-2. Predation equations as per Van Kirk et al. [2010].

Equation	Description
$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_j \sum_b I_{j,b} N_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Predation mortality-at-age for prey species i at age a in year t.
$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Proportion of prey i,a in all food available to predator j,b in year t, assumed equal to the proportion of food within the stomach of predator j,b in year t composed of prey i,a.
$\phi_{i,a,j,b,t} = v_{i,a,j,b} B_{i,a,t}$	Biomass of prey i,a, in year t multiplied by a suitability coefficient v, which defines the probability of predator j,b, selecting for prey i,a.
$\phi_{j,b,t} = B_{oth} + \sum_i \sum_a v_{i,a,j,b,t} B_{i,a,t}$	Total food available in year t to predator j,b, defined as the sum of all available modeled prey plus a constant "Other Food" term which was set to e^{15}.
$v_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b}$	The product of species-preference ρ, and size-preference g. Size-preference g is temporally constant; species-preference can change relative to pooled stomach data.
$g_{i,a,j,b} = \exp\left[-\frac{1}{2\sigma_j^2} \left(\ln \frac{w_{j,b}}{w_{i,a}} - \eta_j \right)^2 \right]$	Size-preference function for predator j,b. Size-preference is constant over a variety of prey species, but g is prey-specific subscripted as prey species differ in size-at-age.

Table 2A-3. Objective function components as per Van Kirk et al. [2010] with the exception of stomach-contents, which were modified for the current work. A caret signifies model estimates.

Equation	Description
$\sum_i \sum_t \left[\ln\left(Ctot_{i,t} + 0.001\right) - \ln\left(\hat{C}tot + 0.001\right)\right]^2$	Total catch (lognormal)
$\sum_i \sum_t \left[\ln\left(Stot_{i,t} + 0.001\right) - \ln\left(\hat{S}tot + 0.001\right)\right]^2$	Total survey (lognormal)
$-\sum_i \sum_a \sum_t \left[\left(\frac{C_{i,a,t}}{Ctot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{C}_{i,a,t}}{\hat{C}tot_{i,t}} + 0.0001\right)\right]$	Catch-at-age (multinomial)
$-\sum_i \sum_a \sum_t \left[\left(\frac{S_{i,a,t}}{Stot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{S}_{i,a,t}}{\hat{S}tot_{i,t}} + 0.0001\right)\right]$	Survey-at-age (multinomial)
$\sum_i \sum_a \sum_j \sum_b \sum_t \left[\left(\sqrt{\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}} + 0.0001\right) - \left(\sqrt{\frac{\hat{\phi}_{i,a,j,b,t}}{\hat{\phi}_{j,b,t}}} + 0.0001\right)\right]^2$	Stomach-contents (root normal)

CHAPTER 3

THE INFLUENCE OF PREDATOR FUNCTIONAL RESPONSES AND INGESTION RATES ON PARAMETER ESTIMATION IN A MULTISPECIES AGE-STRUCTURED ASSESSMENT MODEL[1]

[1]K.F. Van Kirk, T.J.Quinn II, J.S. Collie, and Z.T. A'mar. The influence of predator functional responses and ingestion rates on parameter estimation in a multispecies age-structured assessment model. In preparation to be submitted to Fishery Bulletin

ABSTRACT

Development of effective multispecies models depends on accurately capturing the underlying processes that give rise to sampled populations. Predation is a primary source of mortality for many species, and models incorporating predation mortality should give consideration to the variety of potential behaviors by which predators locate and consume prey. The effects of alternative ingestion rates and predator functional responses on model performance are examined in a multispecies, age-structured assessment (MSASA) model for the Gulf of Alaska (GOA). Modeled species include arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut *(Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). Age-specific predation mortality is estimated as a flexible function of predator and prey abundances, fitted to stomach-content data. Increasing ingestion rates via alternative methods of calculation produced little difference in fit to the objective function, but amplified the effect-per-predator on system dynamics. Predator functional response was observed to be a function of prey abundances as opposed to predator competition or other forms of interaction. The original predator functional response of the GOA MSASA model is shown to be more flexible than originally thought, capable of expressing a variety of predator behaviors.

KEYWORDS: multispecies, predation, Gulf of Alaska, walleye pollock, arrowtooth flounder, Pacific cod, Pacific halibut, Steller sea lion, predator functional response

INTRODUCTION

Predation constitutes the majority of mortality experienced by non-apex marine species (Andersen et al. 2009, Gaichas 2010), often exceeding the biomass removed from commercial fisheries operations (Bax 1998). It would be desirable to have stock assessment models that explicitly incorporate predation functions for the purpose of developing biological reference points robust to predation in a multispecies context (Collie and Gislason 2001, Tyrrell et al. 2011). It follows that understanding the behaviors by which marine predators execute those removals is critical to the development of effective multispecies models.

Two fundamental aspects of predation are ingestion rate and predator functional response. Annual ingestion rate dictates the biomass a predator will consume over the course of a year, and predator functional response defines the manner in which a given predator will feed and meet its metabolic requirements, relative to the abundance of prey and other predators and the manner in which they interact. In conjunction, these two elements contribute to the organization and structure of a given system, especially under predator-controlled (top-down) conditions (Frank et al. 2005).

Correct identification of prey selection and predator behavior are especially important in a multispecies management context, as the modeled response may significantly alter estimates of predation, abundance, and response to commercial fisheries removals (Yodzis 1994). Commercially fished prey species will have different management thresholds if major predators continue to actively seek diminished prey as

opposed to switching to more abundant prey (Mohn and Bowen 1994). By the same token, commercial removals of a given predator species may increase predation on a prey species by reducing competition between predators.

This study examines the effects of alternative annual ingestion rates and the performance of a series of predator functional responses (PFRs) on a multispecies, age-structured assessment (MSASA) model for five species in the Gulf of Alaska (GOA) (Van Kirk et al. 2010, Van Kirk et al. 2012). The MSASA approach integrates the predation equations from multispecies virtual population analysis (MSVPA) (Pope 1979, Sparre 1980) into a statistical, non-deterministic age-structured context. MSVPA assumes stomach-contents to be known without error, while MSASA calculates age-specific predation mortality as a flexible function of predator and prey abundances, fitted to stomach-content data through estimated size- and species-preference parameters.

Model Description

The GOA MSASA model examines the relationships between arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). Sea lions feed primarily on pollock and cod, and marginally on flounder. Halibut target flounder and pollock, as do cod. Flounder are cannibalistic in addition to preying heavily on pollock, while pollock are limited to cannibalism on age 1 pollock (Fig. 3.1).

Abundances for flounder, cod, and pollock are estimated on an annual basis with the MSASA model (January 1 – December 31); model years run from 1981 – 2001 to remain consistent with earlier GOA MSASA model work. Halibut and sea lions function as apex predators with input abundances from external calculations. Data for model fitting (commercial catch, survey results, and sampled stomach contents) are taken from the Alaska Fisheries Science Center (AFSC). To compensate for limited stomach-content data yet still allow for changes in predation due to shifts in predator-prey abundances, stomach-content data for flounder, cod, and pollock are each pooled over seven-year periods into three sets, from 1981 – 1987, 1988 – 1994, and 1995 – 2001. Halibut data are pooled into three sets from 1981 – 1990, 1991 – 1994, and 1995 – 2001, as dictated by sampling events and available data. Very little age-specific data for sea lion diet exists, and much of the literature is unresolved to the scale needed by the MSASA model. Estimated stomach contents for sea lions are therefore bounded by minimum/maximum values extracted from a review of the existing works.

Estimates of predation mortality-at-age in the MSASA model structure are constructed based upon models of size-preference g and species-preference ρ (Van Kirk et al. 2012, 2010). Exact equations for all components of predation mortality are given in Appendix 3A, Table 3A-2. Size-preference is modeled as a log-normal function after Anderson and Ursin (1977) as

$$g_{i,a,j,b} = \exp\left[-\frac{1}{2\sigma_j^2}\left(\ln\frac{w_{j,b}}{w_{i,a}} - \eta_j\right)^2\right] \tag{3.1}$$

in w is weight-at-age of a given predator j of age b, or prey i of age a, η is the optimal log ratio of predator weight-at-age to prey weight-at-age, and σ describes the width of the log-normal distribution, defining the extent to which a given predator j,b will feed on prey i,a of non-optimal size. Size-preference is considered a constant function of physiology – even in the face of temporal variation in weight-at-age, as in the case of halibut, the ratio of a predator weight-at-age to the weight-at-age of optimal prey is assumed invariant. Species-preference ρ is a model parameter and allowed to change over time, with a new value estimated for each time period of pooled stomach-content data. The product of size-preference g from eq. (3.1) and species-preference ρ is termed "suitability" v.

Multiplying suitability v by the biomass B of prey i,a, in year t defines the availability $\phi_{i,a,j,b,t}$ of prey i,a to predator j,b in year t; dividing by the total biomass of all prey available to predator j,b in year t, $\phi_{j,b,t}$ produces the proportion by weight of prey i,a, in the stomach of predator j,b in year t as

$$\frac{v_{i,a,j,b}B_{i,a,t}}{B_{oth}+\sum_{i}\sum_{a}v_{i,a,j,b,t}B_{i,a,t}}=\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}. \tag{3.2}$$

The denominator contains the sum of all modeled prey species and ages available to predator j,b combined with a fixed term B_{oth}, representing the biomass of all other prey not explicitly included in the model structure available to predator j,b. The B_{oth} term was set to e^{15} for initial model fitting, and then refined through calculation of a likelihood profile to $e^{15.825}$. It is assumed that the ratio of available prey i,a to total available prey to predator j,b in eq. (3.2) is equivalent to the proportion by weight of stomach contents of

predator j,b composed of prey i,a. The right side of eq. (3.2) is incorporated into the predation mortality-at-age equation as

$$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_{j} \sum_{b} I_{j,b} N_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} \tag{3.3}$$

in which $I_{j,b}$ is the annual ration (ingestion) in kilograms for predator j,b, and $N_{j,b,t}$ is the abundance of predator j,b, in year t. Total food ingested by all predator j,b is given by the product of $I_{j,b}$ and abundance $N_{j,b,t}$. Multiplying by the availability ratio (3.2) allocates food to each prey species i,a and equivalently to estimated stomach contents. Summing the proportion of stomach contents by weight composed of prey i,a, over all predators j,b, and dividing by the biomass of prey i,a, in year t produces the estimate of total predation mortality P of prey i,a in year t. Further details regarding model construction are found in Van Kirk et al. (2010, 2012); a summary of model equations are presented in Appendix 3A.

METHODS

Ingestion Rate

The rate at which an organism grows (adds somatic tissue) is related to the amount of food consumed over a given period of time, subject to energy losses from metabolic needs, unassimilated food, and metabolic rate (digestion and evacuation). Ingestion rate is a MSASA model input, integral to the estimation of predation. Published

ingestion rates for the modeled species, however, are not abundant. Bioenergetic methods for estimation are still under development and can require data not readily available (Aydin et al. 2007). The GOA MSASA model was originally constructed using the methods of Essington (2001) and Aydin et al. (2007) to estimate annual ingestion rate I for species j, age b as

$$I_{j,b} = \frac{H_j}{A_j} W_b^d , \tag{3.4}$$

in units of kg per year. The parameter A is a measure of assimilation efficiency on the part of a given predator, d and H are allometric parameters governing metabolism and the relationship between age and weight of an organism, and W is the weight of a given species at age b. Work by Aydin et al. (2007) produced values of 0.8 for d, and 0.6 for A. Life-history parameters specific to each modeled species were estimated by fitting observed weights-at-age from AFSC Stock Assessment and Fishery Evaluation (SAFE) reports to an equation for weight-at-age from Essington et al. (2001)

$$W_x = W_\infty \left(1 - e^{-k(1-d)(x-x_0)}\right)^{1/1-d} , \tag{3.5}$$

for which k is the growth coefficient and x_0 the age at which a given species is assumed to have zero weight; values for H were then calculated from these parameters (Table 3.1).

An alternative method for estimating annual ingestion rate can be produced following Hall et al. (2006). This rate is defined as the ratio of annual growth increment (GI) and annual growth efficiency (GE), which is a measure of the efficiency with which an individual produces body mass from consumed food. Annual growth increment is

assumed to come from the von Bertalanffy growth model (Quinn and Deriso 1999) and is given by

$$GI_{j,b} = \left(L_\infty - L_b\right)\left(1 - e^{-k}\right), \tag{3.6}$$

in which L_∞ is the asymptotic species length, L_b is the species length at age b, and k is a growth parameter. Growth efficiency for an individual of predator species j, age b, is defined as

$$GE_{j,b} = 0.5 \left(1 - \left(\frac{w_{j,b}}{w_{j,\infty}}\right)^{0.11}\right), \tag{3.7}$$

in which $w_{j,b}$ refers to mean weight at age for predator j,b, and $w_{j,\infty}$ to the asymptotic weight (Hall et al. 2006). Thus annual ingestion rate is given by

$$I_{j,b} = \frac{GI_{j,b}}{GE_{j,b}}. \tag{3.8}$$

Estimates from eq. (3.8) are larger than those from eq. (3.4), with the difference increasing with fish age (Fig. 3.2).

The above modifications apply to fish species only (halibut, flounder, cod, and pollock). Sea lion ingestion rates utilized in the GOA MSASA model were provided by A. Winship (pers. comm., modifying Winship et al. 2002) from complex bioenergetic studies. The intricacies of that work, in conjunction with limited data regarding sea lion consumption, prevented the development of alternative sea lion ingestion rates in this study. As halibut and sea lions are the apex predators, both with input abundances and the same number of modeled ages, alternative sea lion annual ingestion rates were obtained

by increasing Winship's ingestion rates to the same degree that Hall's methods increased the original halibut ingestion rates.

Four models were assessed for changes due to shifts in annual ingestion rate (Table 3.2):

IR1: the original GOA MSASA model with ingestion rates from eq. (3.4);

IR2: Replacement of the original ingestion rates with those from eq. (3.8) for fish species only; sea lion ingestion rates remain from eq. (3.4);

IR3: Halibut and sea lion ingestion rates come from eq. (3.8); non-apex species (flounder, cod, and pollock) remain at the original levels from eq. (3.4);

IR4: Ingestion rates come from eq. (3.8) for all species.

Predator Functional Response

When fitting to stomach-content data, identifying the correct processes that produced the data is critical to model performance and effective management strategies drawn from it. Predator functional response (PFR) defines the rate at which a predator seeks, encounters, and consumes prey, as a function of prey density, predator satiation limits, competition with other predators, or similar processes (Skalski and Gilliam 2001). Changes in predator behavior, analogous to changes in fishery effort, can alter predation mortality even in the absence of significant variations in prey densities.

The predator functional response most commonly applied to analyses of marine ecosystems is the Holling Type-II response (Holling 1959) (Yodzis 1994), in which

predator response depends on changes in prey abundance and competition between predators is assumed non-existent. Holling expressed predator response in terms of attack rate a (per unit time) and handling time t_h (the time necessary to capture and ingest a given prey item), in which the feeding rate F is the ratio of attack rate divided by the sum of 1 and attack rate times handling time or

$$F = \frac{a}{1 + at_h}, \tag{3.9}$$

(Quinn and Deriso 1999, eq. (1.75)). Within a given time period, the number of consumed prey increases with faster attack rates, shorter handling times, or higher prey density.

The GOA MSASA model incorporates a Holling Type II predator functional response by default (Magnússon 1995). In expanding eq. (3.9) in an age-structured, multispecies context, we assume handling time to be constant, and set attack rate a to be driven by prey density N, setting eq. (3.9) equal to eq. (3.2) as

$$\frac{\text{attack rate}}{\text{attack rate} + \text{handling rate}} = \frac{\text{specific prey available}}{\text{specific prey available} + \text{other prey available}}.$$

Time is set to one year. Suitability v from eq. (3.2) functions as attack rate a from eq. (3.9). Although no such construct as "handling time" exists in the MSASA structure, predation is simply treated as an instantaneous rate for each year. There exists no time between consumption of two separate prey items by a given predator, and each predator j,b is assumed to have identical stomach-contents. We use this Type II PFR as a baseline (PFR1) against which to evaluate the performance of five other potential functional responses when integrated into the GOA MSASA model (Table. 3.3).

The Holling Type II baseline response assumes that predator behavior is a function of prey abundance, as does the Holling Type III (PFR2 below). Other works on functional response posit that predator behavior is influenced by other predators, and generally assume a pool of predators, some seeking prey, and some handling (consuming) prey. The MSASA structure, however, contains no such distinction; all predators are assumed to be handling prey through the suitability coefficient in implementation of the instantaneous rate of predation mortality. When considering the effects of predator competition and interference on predation mortality for prey species i,a , we therefore modify these approaches and distinguish between two groups of predators: those predators with the desire to prey on the target species i and age a in year t, $\theta_{i,a,t}$, and those predators with the desire to seek other prey than i,a in year t, $\lambda_{k,c,t}$.

We define $\theta_{i,a,t}$ as the biomass of all predators with the desire to feed on prey i,a in year t as

$$\theta_{i,a,t} = \sum_{j}\sum_{b} \nu_{i,a,j,b} B_{j,b,t} \,. \tag{3.10}$$

In defining $\lambda_{i,a,t}$, we assume that a predator A cannot interfere with another predator B that is larger than itself, as the interference is the result not of prey depletion (competition for the same prey), but by the perception of potential danger or threat on the part of the predator A when both predators encounter each other in some space also containing a member of prey i,a. Thus $\lambda_{i,a,t}$ is defined as

$$\lambda_{i,a,t} = \sum_{j}\sum_{b}\sum_{k}\sum_{c} \nu_{k,c,j,b} B_{j,b,t} \,, \tag{3.11}$$

in which (k,c) are all prey species and ages $\neq (i,a)$, and b is the age of predator j for which the predator weight-at-age is equal to or greater than the weight-at-age of prey i,a. This condition prevents a given predator B from being influenced by a smaller predator A through implementation of the size-preference function (3.1) and the assumption that a predator cannot prey upon an individual weighing more than itself.

We assessed the following PFR forms (Table 3.3):

PFR1. Holling Type II (asymptotic curve). Default MSASA model structure in eq. (3.2).

PFR2. Holling type III (sigmoid). This form modifies the Holling Type II form of eq. (3.2) to lower the proportions of prey i,a, in the stomach of a given predator j,b at low prey densities (Holling 1959) as

$$\frac{\nu_{i,a,j,b}\left(B_{i,a,t}\right)^2}{B_{oth}{}^2+\sum_j\sum_b \nu_{i,a,j,b}\left(B_{i,a,t}\right)^2}=\frac{\phi_{i,a,j,b,t}B_{i,a,t}}{B_{oth}{}^2+\sum_j\sum_b \phi_{i,a,j,b,t}B_{i,a,t}}. \tag{3.12}$$

PFR3. Predator interference. Developed by both Beddington (1975) and DeAngelis et al. (1975), this form assumes that predator seek/encounter rates are affected by the seeking of other predators; a predator that is handling (consuming) prey is assumed to contribute no interference. As above, this distinction is not included in the MSASA structure, and we therefore modify the approach as

$$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}+\gamma_{ji}\lambda_{i,a,t}}, \tag{3.13}$$

in which γ is a model-estimated positive constant defining the degree to which predation mortality-at-age on prey i,a, is influenced by predator interference. A γ parameter is estimated for each predator species j, and it is assumed that each

predator species *j* will have the same interference response regardless of prey species or age. Beddington's original paper subtracted 1 from the total predator abundance with the assumption that a predator cannot interfere with itself, while DeAngelis et al. did not. Here we follow the suggestion of Skalski and Gilliam (2001) that when predator abundance is modeled as a continuous variable, simply using total predator abundance is more appropriate.

PFR4. Predator competition. Here we reverse PFR3, and assume that predators targeting different prey do not interfere with each other, but that predators targeting the same prey-at-age will compete for prey and thereby affect functional response, as

$$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t} + \gamma_j \theta_{i,a,t}} \tag{3.14}$$

in which the gamma coefficient is as in eq. (3.13).

PFR5. Predator pre-emption. Crowley and Martin (1989) modified the interference response form PFR3 by removing the assumption that handling and interference are mutually exclusive and that regardless of activity, a given predator can interfere with other predators as

$$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t} + \gamma_i(\lambda_{i,a,t} + \theta_{i,a,t})} \tag{3.15}$$

in which γ is as in eq. (3.13), and consumption of prey *i,a*, is affected by the total density of predators regardless of activity

PFR6. Hassell-Varley. An alternative form of predator interference similar to PFR 5 incorporates an exponential form of predator density-dependence as

$$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t} + \left(\lambda_{i,a,t} + \theta_{i,a,t}\right)^{\gamma_i}}, \tag{3.16}$$

in which γ remains an indicator of the magnitude of predator interference (Hassell and Varley, 1969 *in* Skalski and Gilliam, 2001).

The default GOA MSASA model structure allows for changes in the species-preference parameter ρ, enabling changes in predator behavior relative to shifts in relative predator-prey abundances. As these changes may potentially be better represented by the PFR forms above, rendering a dynamic ρ parameter redundant, we therefore replicate each of the six PFR forms above (including the baseline PFR1) under conditions in which a single ρ parameter is estimated for all modeled years, designated as PFR1R, PFR2R, PFR3R, etc.

Another PFR, widely used in ECOPATH modeling, was developed by Walters and Kitchell (1997), in which prey have the capability of inhabiting temporal or spatial refuges that reduce or eliminate predator access. This form was explored in a multispecies context by Koen-Alonso and Yodzis (2005) and in an age-structured multispecies context by Kinzey and Punt (2009). Both works founds this approach to have the poorest performance of all modeled PFR forms. Given their results, and given that the GOA MSASA model has no explicitly defined spatial component nor does its annual dynamics allow for modeling sub-annual migrations of prey species to potential temporal refuges either topographically or by virtue of increased abundance (i.e., pollock spawning aggregations), we did not include this form in those examined below.

The examined PFRs apply to the modeled fish species only. The goal behind including various PFRs in our model is to allow discovery of underlying forms driven by information contained within sampled stomach-content data. As discussed above, however, almost no age-informative stomach-content data exist for sea lions, and any attempt at defining a valid PFR by virtue of the minimum/maximum bounds set on sea lion on feeding habits would be a circular exercise, and we therefore kept sea lion predation in the original GOA MSASA model form (PFR1).

All explorations of PFR forms were implemented using the annual rations from the original GOA MSASA model (IR1).

Aikike Information Criterion (AIC) values, defined as $-2\ln L - 2p$, in which $\ln L$ is the negative log-likelihood value from each model and p is the number of estimated parameters, were used for initial evaluation of PFR model results.

RESULTS

Ingestion Rate

Compared to IR1, increasing annual ingestion rates for fish species in IR2 had the straightforward effect of increasing predation on pollock (Fig. 3.3) and to a lesser degree on flounder (Fig 3.4). Predation was heaviest on younger prey ages, with the attendant result that increases in abundance were primarily for those ages, while total annual biomass was roughly the same between IR1 and IR2 (Fig. 3.5). Residual natural

mortality M_0 for flounder, cod and pollock increased (Fig. 3.6), although the increase for cod and pollock was very slight. Cohort structure (relative abundance of age classes) remained largely unchanged for older prey ages, as evidenced by lack of change in fishery selectivities, full recruitment fishing mortality F, and predator size-preference curves (not shown). Survey selectivities for flounder and pollock shifted only slightly and the age of peak selectivity remained the same for each species. Objective function values between IR1 and IR2 were virtually identical. As no changes to sea lion annual ingestion rate were implemented in IR2, cod populations remained mostly unchanged (Fig. 3.5), and predation mortality on cod remained the same (Fig. 3.7).

IR3 displayed different dynamics than IR1 and 2 due to the selection of older prey by sea lions and the increased ingestion rate of sea lions and halibut. While predation on ages 2 -5 pollock remained higher than IR1 due to increases in halibut predation, mortality on age 1 declined due to reduced cod abundance as a result of sea lion predation (Fig. 3.3). Total annual abundance and biomass for pollock and flounder were closer to IR1 levels than IR2, while abundance and biomass for cod were smaller (Fig. 3.5). The decline in cod abundance was for ages 1 - 5, at which point age-specific estimates from IR3 coincided with those from IR1 and 2 (not shown). Residual natural mortality M_0 for flounder was the same as for IR1, while M_0 for both cod and pollock dropped markedly (Fig. 3.6). Fishery selectivities remained as in IR1, as did size-preference curves, while F values for pollock and cod showed only small changes from baseline values. Pollock survey selectivities were as in IR2, while flounder reverted to IR1 values; cod changed only slightly from both Model IR1 and 2. Predation pressure from cod and flounder on

their respective prey species remained the same as in IR1, while predation from halibut was the same as in IR2, and sea lion predation increased as expected on older pollock (Fig. 3.3) and cod (Fig. 3.7).

IR4 levied the highest predation on all species, producing the highest overall predation on pollock and flounder although peak predation on age 1 flounder was lower than in IR2 (Fig. 3.4). Abundances for prey species, including cod, were elevated to IR2 levels (Fig. 3.5). M_0 values for cod and flounder were as in IR3, but M_0 values for pollock dropped to the lowest of all ingestion rate models (Fig. 3.6). Predation pressure on cod was similar to IR3 and larger than IR1 and IR2 (Fig. 3.7).

Predator Functional Response

In general, PFR models that used a single species-preference value performed worse (higher AIC value) than their counterparts in which ρ was allowed to change relative to changes in stomach-content data (Table 3.4). PFR3 and PFR5 produced AIC values similar to the baseline PFR1 value. The worst performance came from PFR2R (followed by PFR2), and the best from PFR4, in which the AIC value of 1847 was 38 less than the baseline AIC of 1885.

Objective function (OF) values for catch and survey datasets differed little between PFR models (not shown). Examination of stomach-content OF components showed that changes in fits to flounder and cod stomach-content data (Fig. 3.8),

especially in Period 3 (1995 – 2001) were the primary means by which AIC values were increased or reduced.

Estimates of total annual biomass were similar between the baseline PFR1, the worst model PFR2R, and the best scoring model PFR4 (Fig. 3.9); other model estimates fell between PFR2R and PFR4 estimates (not shown).

Halibut predation on pollock was drastically different for PFR3 and PFR 5 (Fig. 3.10a) relative to other models. Cod predation on pollock was different in PFR4 relative to other models, showing increased selection for older pollock (Fig. 3.10b). Trends in predation mortality-at-age on pollock from flounder and sea lions were similar between PFR models, although PFR 4 showed reduced predation on age-1 pollock from flounder which was not observed in other models (Fig. 3.10c, d). Predation mortality-at-age for flounder from halibut showed similar disparities between PFR3 and PFR5 relative to other models (Fig. 3.11a). Cod predation on flounder was reduced markedly from other models in PFR 4 (Fig. 3.11b). Trends in flounder cannibalism trends were similar between models (Fig. 3.11c).

Size-preference curves were similar between models with the exception of PFR4, in which cod size-preference shifted towards larger prey; changes in predation were otherwise driven by the implemented PFRs and shifts in species-preference coefficients (not shown). Flounder displayed higher species-preference for pollock even during periods of low pollock abundance, while cod species-preference coefficients tended to be higher for prey species with higher abundance.

Examination of values for the predator-competition parameter γ in the model with the best performance (PFR4) showed values close to zero for flounder and halibut, but much larger for cod.

Predation mortality-at-age was found to be roughly proportional to the ratio of competing predators $\theta_{i,a,t}$ to the biomass of prey i,a as $\theta_{i,a,t}/B_{i,a,t}$ from PFR4 (Fig. 3.12) although formal derivation of this property was not reached. Predator-to-prey ratios from PFR3 using $\lambda_{i,a,t}/B_{i,a,t}$, and PFR5 and PFR6 using $(\lambda_{i,a,t}+\theta_{i,a,t})/B_{i,a,t}$ did not follow predation trends as well. This proportionality was also observed to be applicable primarily to younger ages; predation mortality on older prey (Fig. 3.13) did not show the same visual correlation to predator-prey ratios for any PFR model.

DISCUSSION

Ingestion Rate

Criteria by which to select an ingestion rate model do not appear to be straightforward. All four models produced similar fits, and while estimates of biomass varied to some degree, no performance indicators served to differentiate between them. This was due partially to the precedence given to fitting catch and survey data sets through heavier weighting in the objective function, resulting in similar model performance across configurations. It is also evidence of the manner in which predation mortality, residual natural mortality, and survey selectivity are confounded (Thompson

1994, Van Kirk et al. 2012). Increased ingestion by fish predators resulted in increased recruitment, which can be partitioned off into predation mortality without change to cohort structure provided that predator consumption of each prey age is proportional to the relative increase, with both increase and consumption declining over age. Predation on pollock increased linearly for younger ages in IR2 relative to IR1, displaying the same slope (Fig. 3.2), and M_0 showed no change between models (Fig. 3.5). Predation on flounder, however, was not a monotonic increase over younger ages, but showed an irregular dip in predation on age 2, while predation was similar for ages 1 and 3 (Fig. 3.3). This resulted in the increase in age 1 abundance being passed through age 2 without removal due to predation, and required an increase in M_0 (Fig. 3.5) to maintain the cohort structure necessary for fitting to catch and survey data. Increased annual ingestion rate for sea lions, which feed on older prey instead of younger, resulted in lower M_0 values in IR3 and IR4 (Fig. 3.5) because the biomass of those older ages was consumed, as opposed to removal from M_0. Where sea lion predation pressure was heaviest on the oldest cohorts (i.e., pollock), no increase in recruitment was observed for IR3. Where sea lion predation was heaviest on intermediate ages (cod), both recruitment and M_0 were significantly reduced.

Annual ingestion rate determines the extent of predation mortality per predator. Higher ingestion rates amplify this effect and increase system sensitivity to perturbations from commercial fisheries removals. For example, multiplying model-estimated commercial catch-at-age for Pacific cod in the GOA in 2000 by the appropriate age-specific ingestion rates from Aydin et al. (2007) produces a figure of 34.31 metric tons of

prey species that would have been consumed had those cod not been removed by fishing activities. The same exercise using the ingestion rates from Hall et al. (2006) produces a figure of 54.11 metric tons, an increase of over 50%. Stock assessments using the former ingestion rates would estimate 50% more prey remaining in the Gulf of Alaska than assessment using the latter, potentially affecting harvest limits. Cod feed upon flounder, which in turn feed heavily on pollock. Thus, the commercial cod fishery might contribute to the decline of pollock stocks by removing cod which might aid in controlling flounder abundance and therefore predation on pollock. This heightened sensitivity affects estimates of the strength of species linkages and the assessment of fishing mortality in a multispecies context. While these issues are fundamental to the construction of effective multispecies models, selection of an appropriate ingestion rate remains somewhat *ad hoc*. We plan to continue implementation of the original GOA MSASA model ingestion rates as per eq. (3.5). Many current research projects examining GOA species and systems use the same approach, and as these are often used in advisory capacity to stock assessment efforts (i.e. Aydin et al. 2007, Gaichas et al. 2010), maintaining methodological homogeneity enables better cross-model comparison and integration of results.

Predator Functional Response

The performance of a given PFR is influenced by the pooled stomach data and annual time step of the GOA MSASA structure. Pooling was necessary to compensate for missing data and years in which no sampling surveys were undertaken. During early

model development, we experimented with fitting to unpooled stomach data for each year for which they were available, but the annual data were too sparse to permit parameter estimation. Predator functional responses, however, are active over a finer scale than the pooled data (Levin 1992), and the fluctuations of predator and prey abundances are therefore potentially obscured when fitting to pooled data. While survey and composition data contain some of this information, not explicitly accounting for PFR dynamics over the appropriate temporal scale can result in erroneous model conclusions regarding selectivity and survey catchability. The spawning aggregations of pollock, for example, provide a time in which predator response may shift relative to increased local prey availability, and such spatio-temporal variability is lost in the GOA MSASA model structure. In addition, age-structured approaches enable consideration of age-dependent changes in predator-prey interactions, in which older cohorts of a prey species may feed upon younger ages of a predator (Walters and Kitchell 2001). This produces potential positive feedback between predator and prey species, which may serve to obscure predator feeding dynamics. The assumption of sufficient food in all years for all predators (through the implementation of the 'Other Food' component in eq. 3.2) may also limit the application of competition-based functional responses in models of this structure.

It appears that a static species-preference parameter (R models) is unable to adequately capture variability in predator diet composition even with the explicit implementation of a predator functional response. Prey-switching is likely to be predator-specific: a generalist predator might be expected to direct feeding pressure on more abundant prey regardless of species, whereas a specialist would continue to pursue

specific prey even in the face of reduced abundance. For a generalist predator, then, a simple Holling Type II or III PFR might be sufficient to encompass diet variability, whereas the behavior of a specialist would not be adequately represented by such a PFR and require at the very least a flexible species-preference parameter. Magnússon (1995) showed that the basic form of eq. (3.4) results in a Holling Type II functional response, as the relative proportion of any specific prey species and age in a given predator's diet is reduced as total available prey increases. This assumes, however, that the species-preference coefficient ρ remains constant. Upon consideration, the estimation of a ρ parameter for each separate prey period changes the overall PFR of the baseline MSASA configuration (PFR1) across all modeled years to a much more flexible format. Prey switching can be forced by any number of factors that are involved with the stomach-content data, including by diminishing prey abundance, active seeking of reduced prey, reduced seeking of increasing prey (higher encounter rate), or prey switching due to some form of predator competition. Each of these processes can indicate a different form of predator functional response, even if the actual underlying PFR structure is poorly understood. This flexibility reduces the constraints on model performance due to the assumption of homogenous distributions of predator and prey, although it is able only to encompass large-scale temporal shifts in behavior and not sub-annual fluctuations such as in pollock spawning aggregations, and within each time period the PFR reduces to a Type II response. As stomach sampling continues with new sets of data generally available every two-three years, allowing the species-preference parameters to change for each new data set would enable the greatest model sensitivity to changes in predator behaviors.

The results suggest that competition between predators targeting the same prey-at-age $\theta_{i,a,t}$ (PFR4) is an important factor in accurately identifying and modeling predator functional response in the Gulf of Alaska. The $\lambda_{i,a,t}$ coefficient for spatial interference, however, was much less effective (PFR3) in explaining the stomach data, and although such interference may play a role in predator behavior, it seems less relevant than direct competition (PFR 4). It may also be that the λ group of predators contains such a wide array of predator species and ages that any relevant signal is obscured by statistical noise. Improved function might possibly be achieved through development of an alternative method for defining and selecting members of this group. When both predator groups were combined (PFR5, PFR6), the signal contained in the $\theta_{i,a,t}$ group was overwhelmed and weakened by the noise of the larger group $\lambda_{i,a,t.}$

Moustahfid et al. (2010) found that variations of Holling Type II and III responses were the most common among the northeast US continental shelf species examined in their work. Similarly, Koen-Alonso and Yodzis (2005) determined that predator-independent forms of PFR provided the best fit to survey and catch data in a trophodynamic multispecies model for the southwest Atlantic Ocean. Different results were obtained by Skalski and Gilliam (2001) and Kinzey and Punt (2009). Both found PFR5 to perform better than a Holling Type II PFR in the systems they examined, and Skalski and Gilliam (2001) also found PFR6 to be applicable under conditions of simultaneously high prey abundance and high predator density. Kinzey and Punt's approach is more similar to the GOA MSASA model than the other cited works, in that it is age-structured, was applied to similar species in relatively close geographical

proximity, and fitted daily consumption rate estimates to calculations from Essington et al. (2001). This study, however, showed PFR5 to have a performance similar to the baseline PFR1, rather than better. The reason for this disparity remains unclear, although Kinzey and Punt followed the classical forms of predator functional response (after Skalski and Gilliam 2001) and did not make the distinction between the two predator groups of this study. In addition, Kinzey and Punt assumed equilibrium between populations during the first year of their model, which this study does not.

PFR4 showed the lowest AIC score and the most improvements to flounder and cod objective function components, but the changes in cod predation on pollock were drastically different from other models. According to this model, cod apparently function as generalist predators, and are also influenced by other predators competing for the same prey, as indicated by the better fit of PFR4. Predation on younger prey cohorts is generally higher than older cohorts, implying a larger pool of predators seeking those prey and a declining value for θ from eq. (3.14) as prey age. Taken in combination, these factors support the observed move towards larger prey on the part of cod in PFR4, focusing on a prey group with fewer overall predators and therefore less competition. Skalski and Gilliam (2001) found that no individual PFR described all predator behavior, and Moustahfid et al. (2010) showed that a given predator may display different responses to different prey species. The observed pattern of increasing prey-preference for pollock by flounder in the face of decreasing pollock abundance suggests a predator actively seeking a specific prey, whereas the changes in cod preference for pollock imply a generalist predator with hunting patterns dictated primarily by encounter rate.

The complex synergism of PFRs in a multispecies context likely makes consistent detection of prey-switching and other predator behaviors difficult (Hixon and Carr 1997). We therefore recommend that age-structured multispecies models be initially constructed with the default Holling Type II predator functional response until sufficiently informative stomach-content data become available to implement appropriate forms of PFR4 for each predator species.

The issue of minimal sufficient complexity in model development is ongoing (Punt and Leslie 1995, Fulton et al. 2003), and depends partially on data availability as well as the aims of a given model structure. For multispecies models using age-structure of predator and prey, incremented on an annual time-scale for which sufficient stomach-content data are available, the GOA MSASA model structure should provide a robust yet flexible tool for modeling predation. Further work along both temporal and spatial scales, in conjunction with additional diet data, should allow it to continue development into a practical tool for multispecies stock assessment.

ACKNOWLEDGMENTS

This work was funded by the Pollock Conservation Cooperative Research Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the Center or the University of Alaska.

This publication is also the result of research sponsored by Alaska Sea Grant with funds provided by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-11, 14), and from the University of Alaska with funds appropriated from the State.

This publication is also the result in part of research and education sponsored by the Cooperative Institute for Arctic Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA17RJ1224 with the University of Alaska.

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Table 3.1. Estimated H values for pollock, cod, flounder, and halibut from eqs. (3.4, 3.5).

	Pollock	Cod	Flounder (female)	Flounder (male)	Halibut (temporally variable due to changes in weight-at-age)
H values	1.67	1.28	5.09	2.93	2.23 – 3.67

Table 3.2. Summary of model conditions used to evaluate the effects of increased annual ingestion rates.

MODEL	CONDITIONS
IR1	The original GOA MSASA model with ingestion rates from eq. (3.4).
IR2	Replacement of the original ingestion rates with those from eq. (3.8) for fish species only; sea lion ingestion rates remain from eq. (3.4).
IR3	Halibut and sea lion ingestion rates come from eq. (3.8); non-apex species (flounder, cod, and pollock) remain at the original levels from eq. (3.4).
IR4	Ingestion rates come from eq. (3.8) for all species.

Table 3.3. Summary of model conditions used to evaluate predator functional responses. For each form listed, an alternate PFR using a static species-preference parameter ρ was also tested (identified with an R in the text).

MODEL	CONDITIONS
PFR1(R)	Baseline GOA MSASA functional response: Holling Type 2.
PFR2(R)	Holling Type III response
PFR3(R)	Predator interference when seeking other prey (Beddington 1975, DeAngelis 1975)
PFR4(R)	Predator competition when seeking the same prey (Beddington 1975, DeAngelis 1975)
PFR5(R)	Pre-emption: predator interference under all conditions (Crowley and Martin 1989)
PFR6(R)	Pre-emption: predator interference under all conditions (Hassel-Varley 1969)

Table 3.4. AIC values for all PFR models in ascending order

Model	AIC
PFR4	1848.88
PFR6	1870.59
PFR5R	1878.63
PFR3	1884.25
PFR3R	1884.91
PFR1	1885.61
PFR5	1885.78
PFR4R	1893.29
PFR6R	1902.19
PFR1R	1910.68
PFR2	1933.81
PFR2R	1953.71

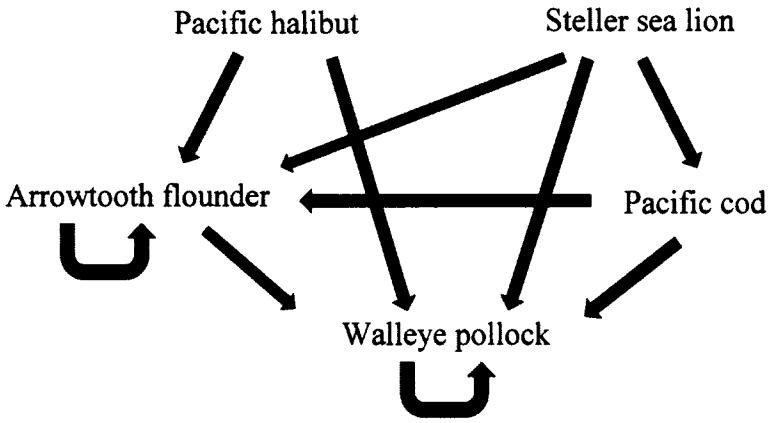

Figure 3.1. Predation linkages in the GOA MSASA model as per Van Kirk et al. (2012); curved arrows indicate cannibalism.

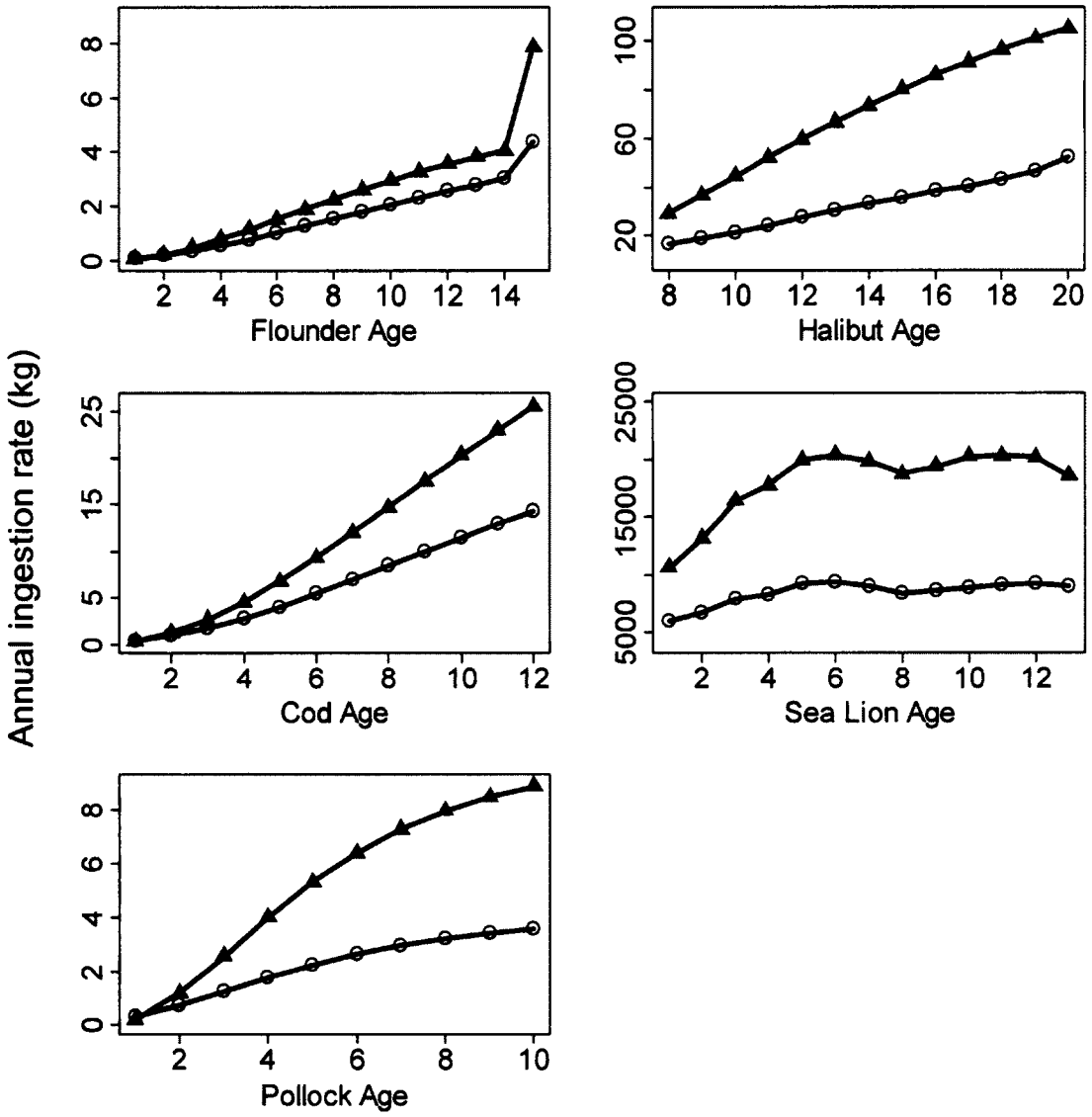

Figure 3.2. Annual ingestion rates for each species in kilograms consumed. Estimates based on eq. (3.5) (Aydin et al. 2007) are circles; triangles based on estimates from eq. (3.9) (Hall et al. (2006).

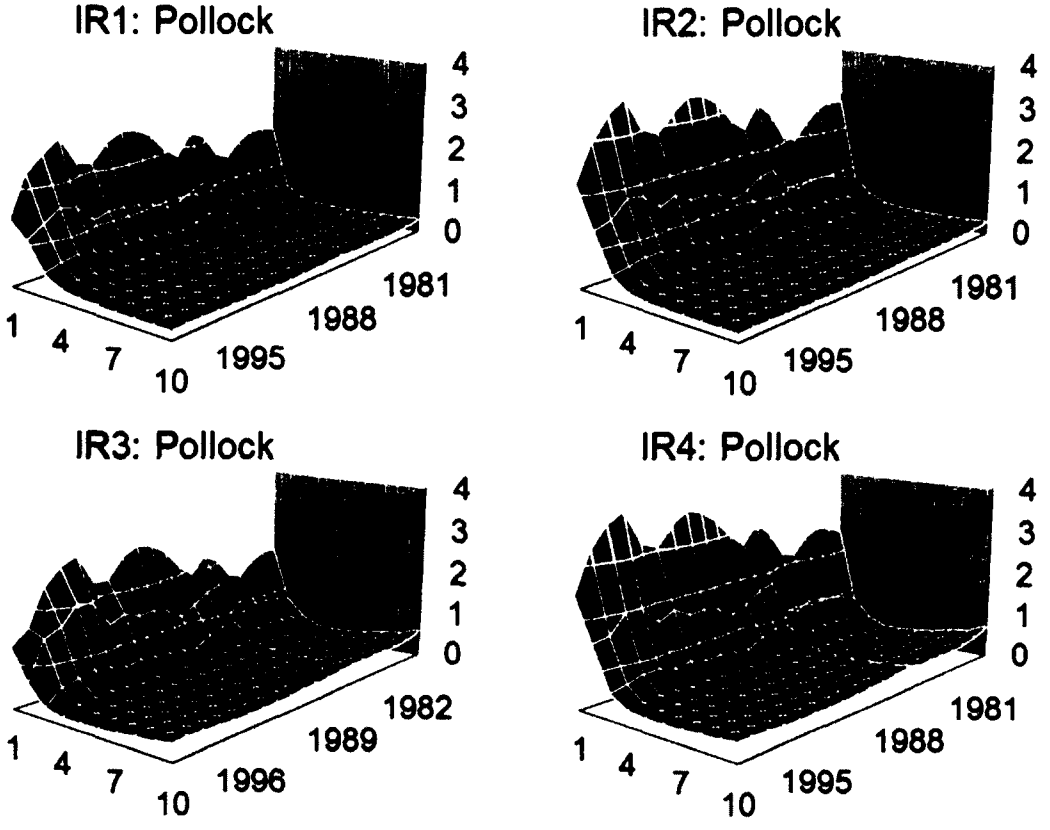

Figure 3.3. Total predation mortality on pollock from IR1 – IR4, with year on the x-axis, prey age on the y-axis, and predation mortality on the z-axis.

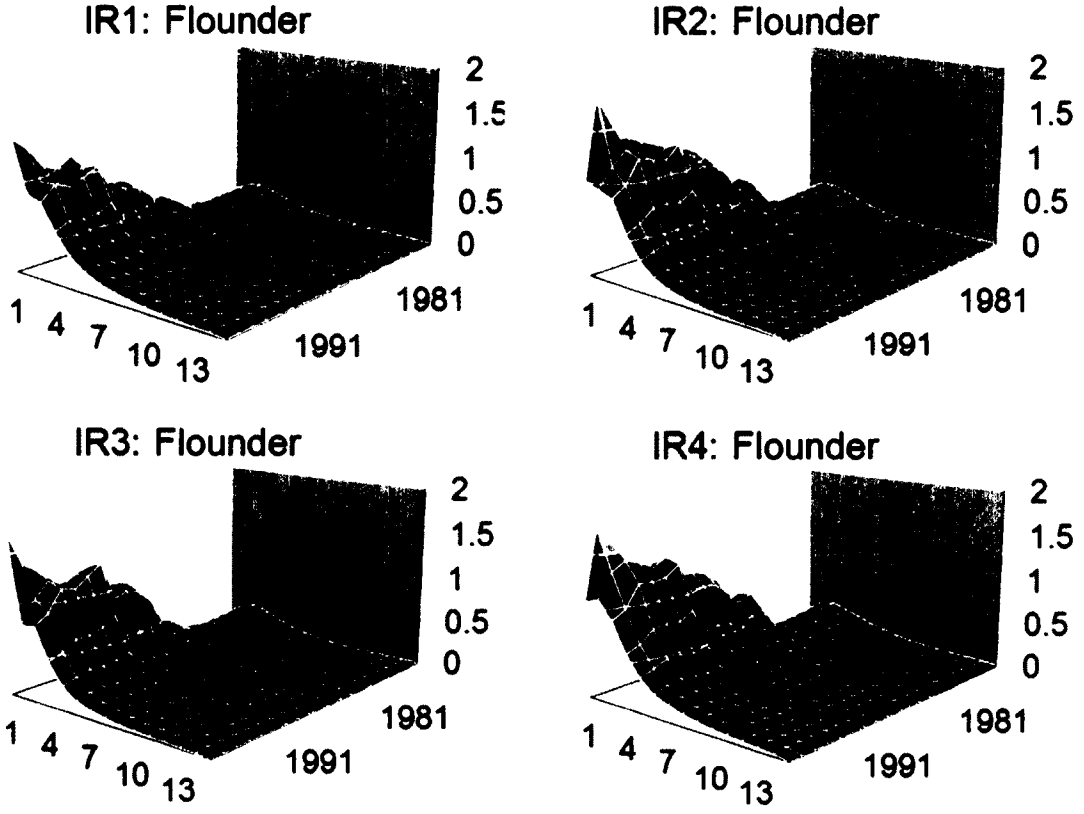

Figure 3.4. Total predation mortality on flounder from IR1 – IR4, with year on the x-axis, prey age on the y-axis, and predation mortality on the z-axis.

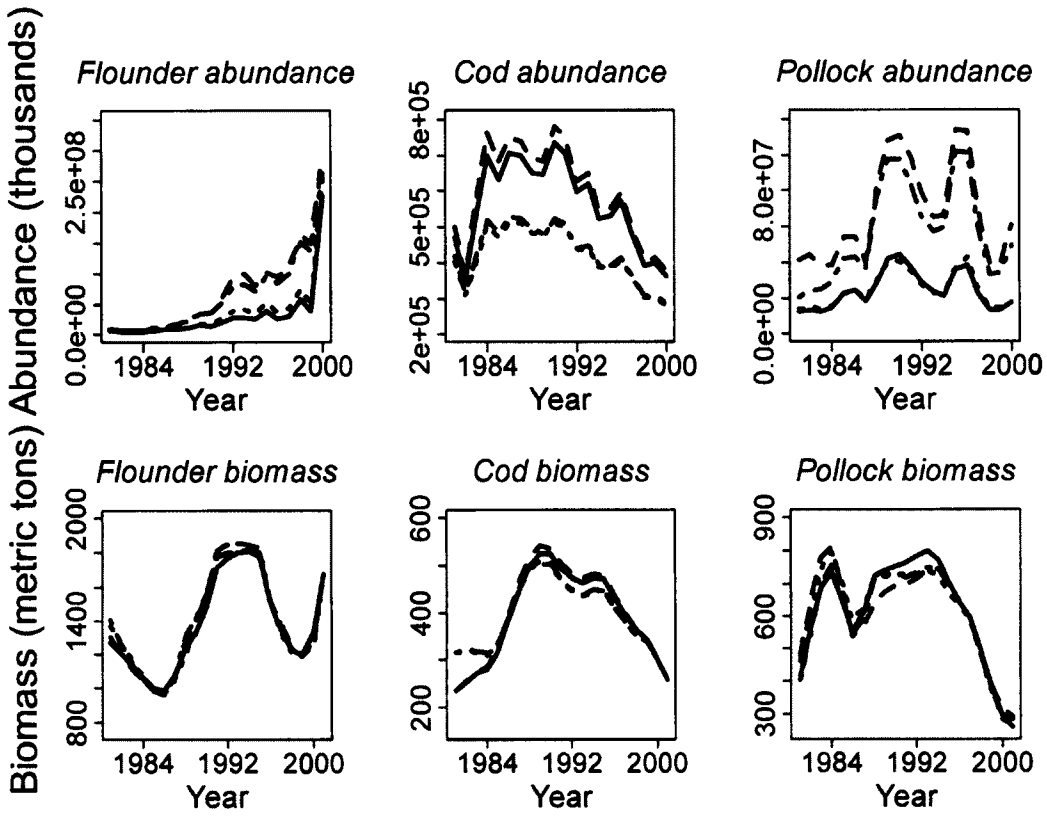

Figure 3.5. Total annual abundance and total annual biomass for flounder, cod, and pollock from IR1 – IR4. Solid = IR1, dashed = IR2, dotted = IR3, dot-dash = IR4.

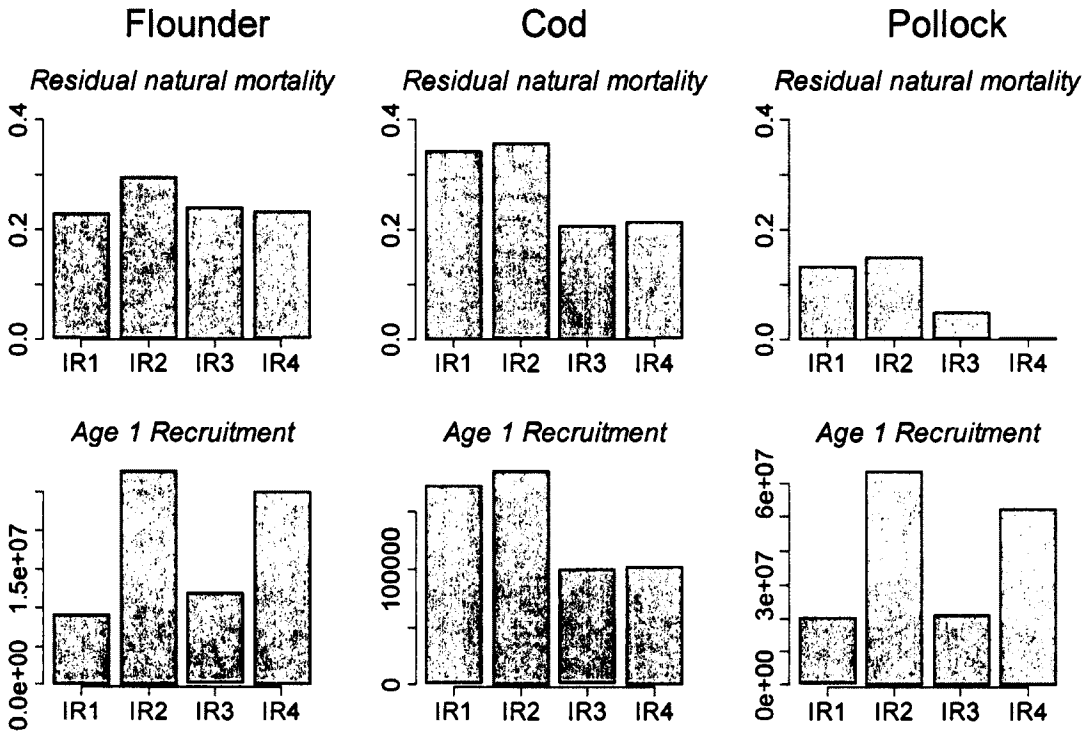

Figure 3.6. Residual natural mortality M0 and age-1 recruitment for flounder, cod and pollock, averaged over all model years, IR1 – IR4.

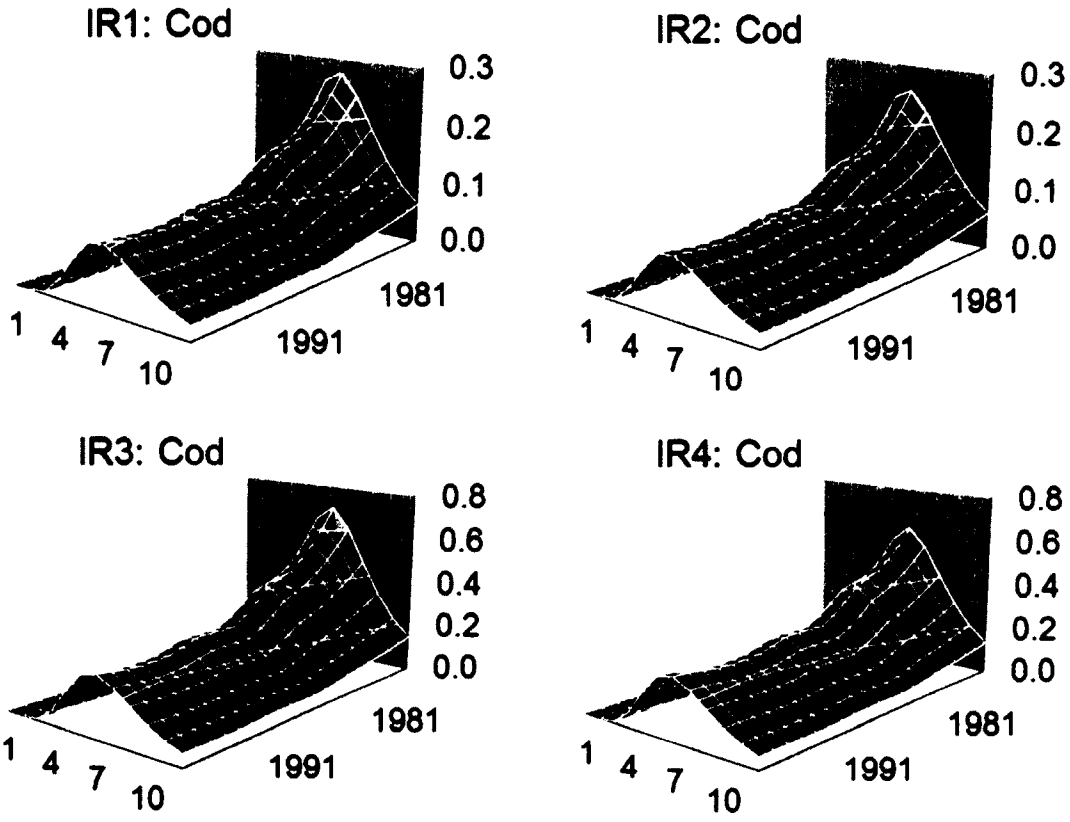

Figure 3.7. Total predation mortality on cod from IR1 – IR4 , with year on the x-axis, prey age on the y-axis, and predation mortality on the z-axis.

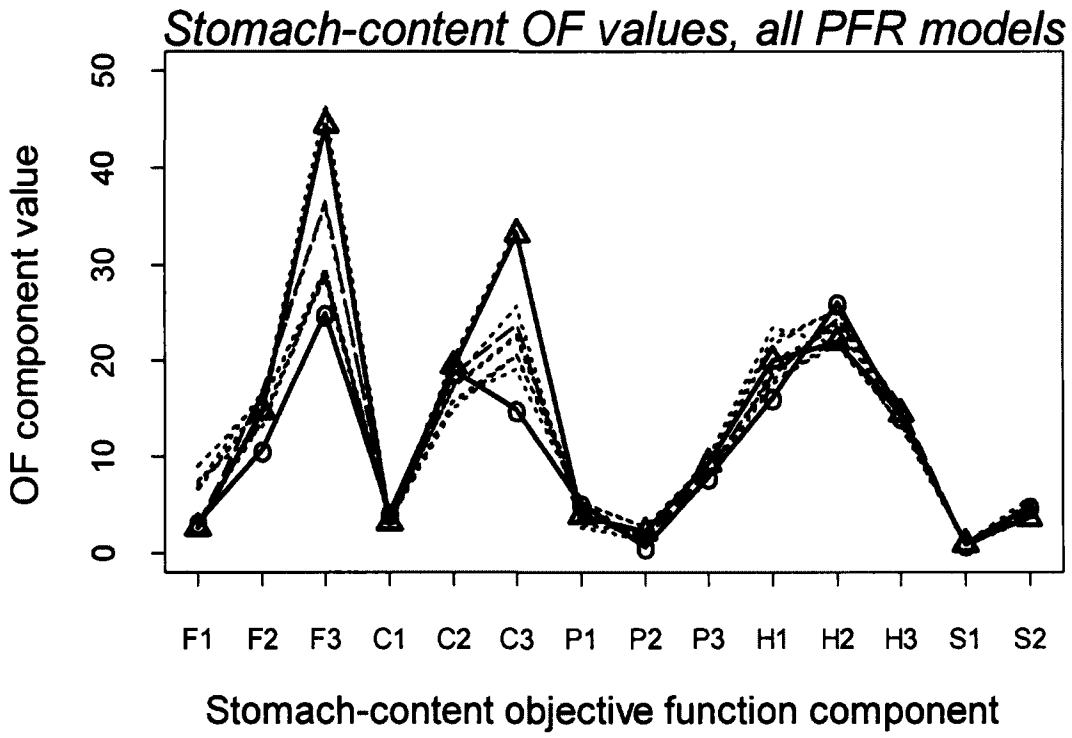

Figure 3.8. Objective function (OF) values for stomach-content components for all PFR models. Circle = best fitting PFR 4 model, triangle = poorest fit PFR 2R model; all others unmarked. F = flounder, C = cod, P = pollock, H = halibut, S = sea lion, 1 = pooling period 1 (1981 – 1987), 2 = pooling period 2 (1988 – 1994), 3 = pooling period 3 (1995 – 2001) except for sea lion, for which 1 = minimum stomach-content bound, 2 = maximum.

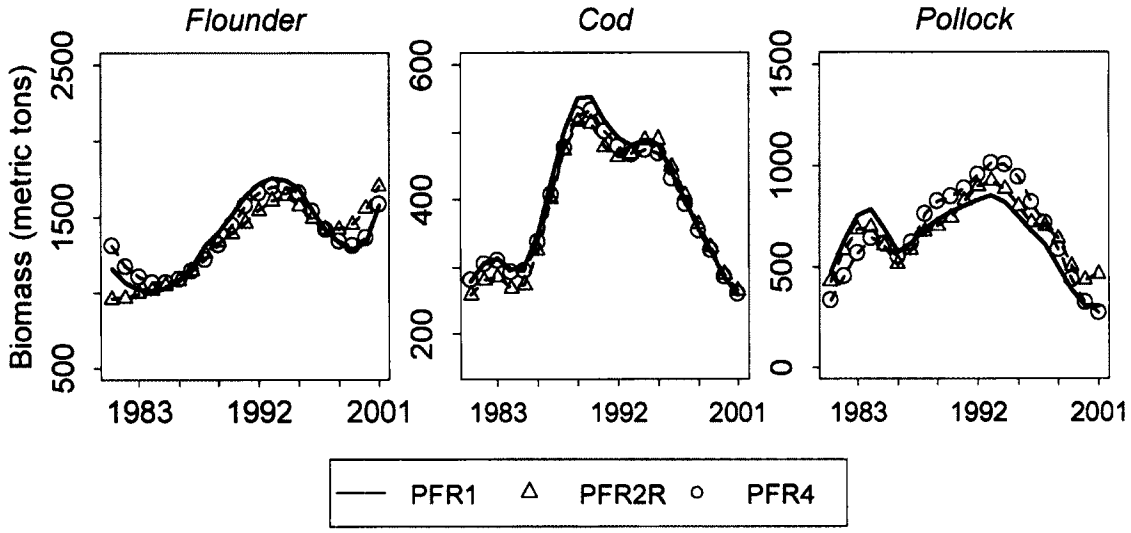

Figure 3.9. Estimates of total annual biomass for flounder, cod and pollock from PFR1 (baseline Holling II response), PFR2R (Holling III, single species-preference, poorest PFR fit), and PFR4 (best PFR fit, predator interference from seeking same prey).

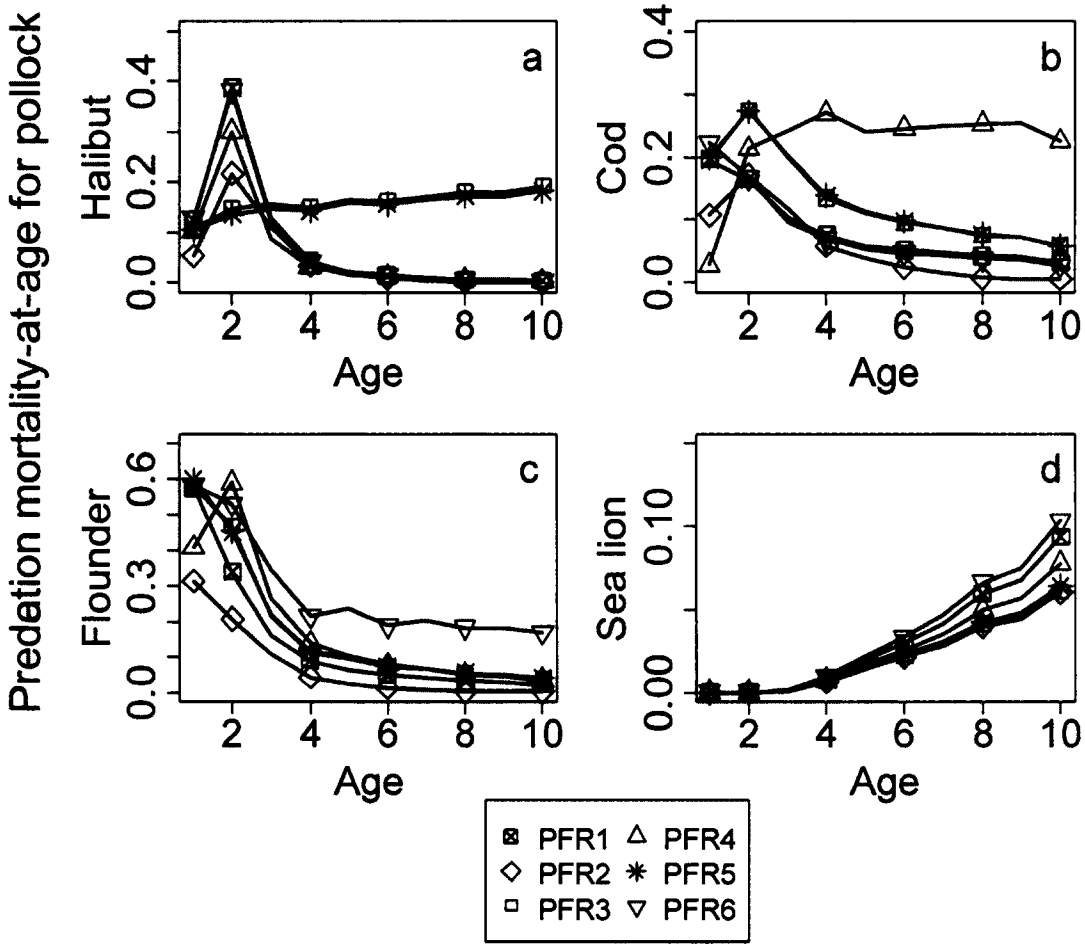

Figure 3.10. Predation mortality-at-age on pollock from PFR1 – PFR6 averaged over all model years from (a) halibut, (b) cod, (c) flounder, and (d) sea lions; R replicates not shown.

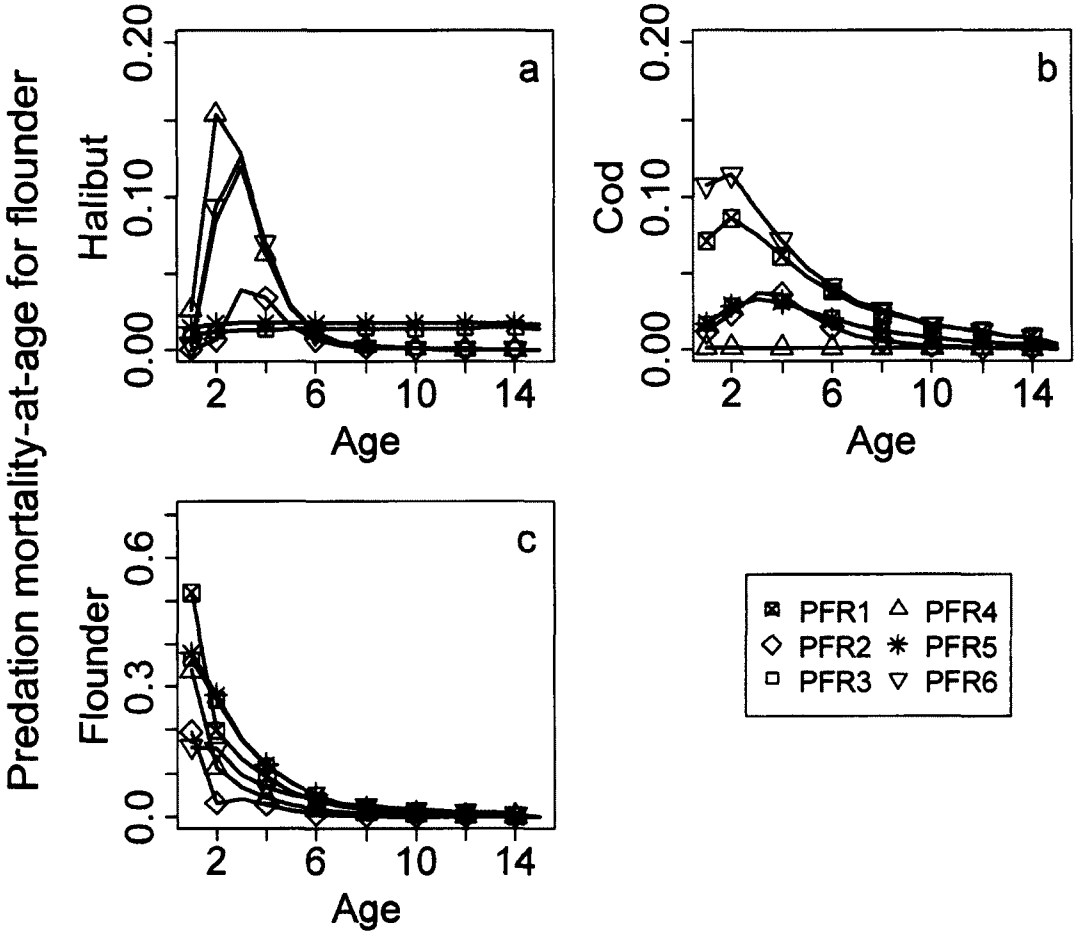

Figure 3.11. Predation mortality-at-age on flounder from PFR1 – PFR6 averaged over all model years from (a) halibut, (b) cod, (c) flounder; R replicates not shown.

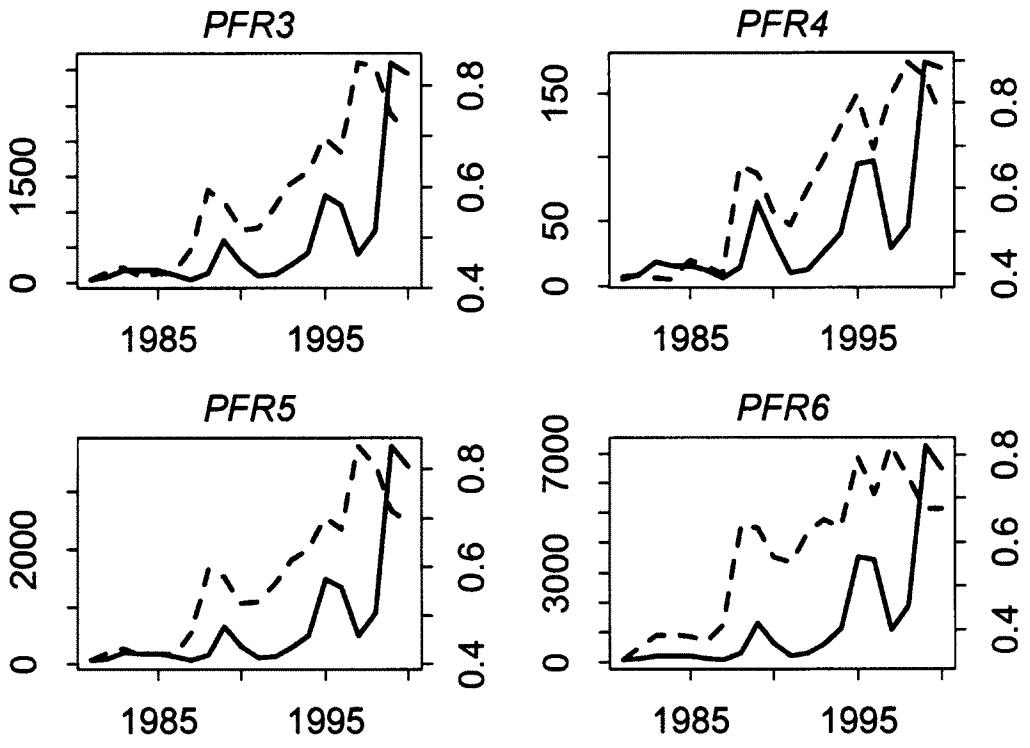

Figure 3.12. Predation mortality on age 3 pollock (dashed line, second y-axis) plotted against the sum total of all predators on age 3 pollock divided by the abundance of age 3 pollock (solid line, primary y-axis) for each modeled year from PFR 3 – 6 (predator-density functional responses).

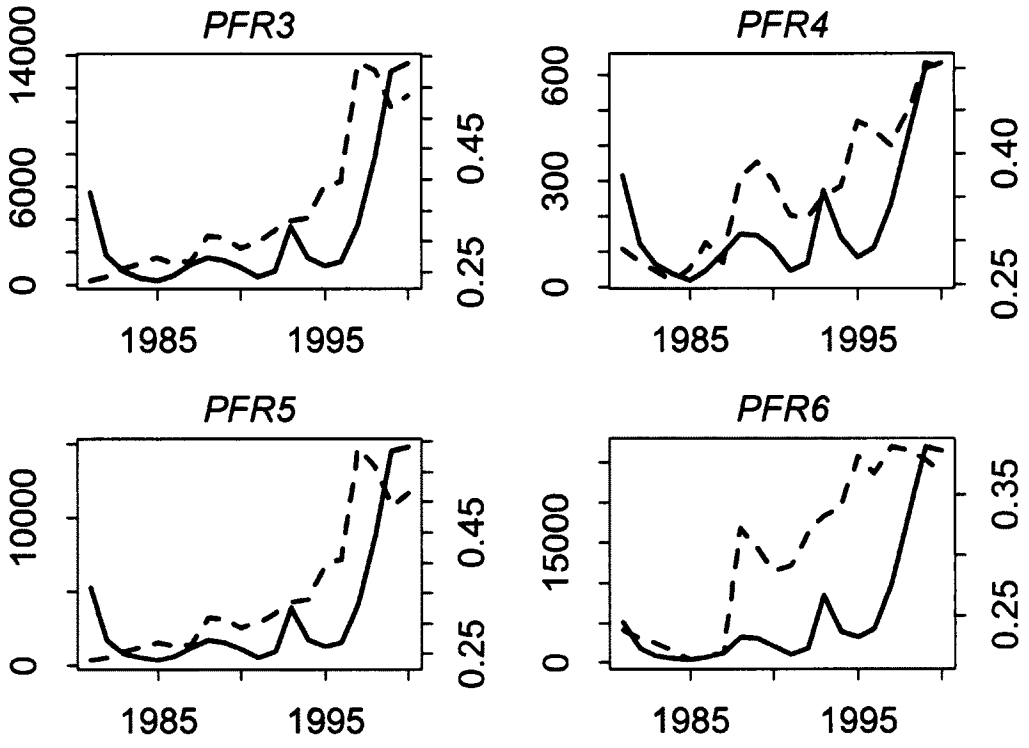

Figure 3.13. Predation mortality on age 7 pollock (dashed line, second y-axis) plotted against the sum total of all predators on age 7 pollock divided by the abundance of age 7 pollock (solid line, primary y-axis) for each modeled year from PFR 3 – 6 (predator-density functional responses).

APPENDIX 3A

Data sets and equations for construction of the Gulf of Alaska multispecies age-structured assessment model as per Van Kirk et al. (2010)

Table 3A-1. Population dynamics equations as per Van Kirk et al. [2010] and Quinn and Deriso [1999].

Equation	Description
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}}$	Abundance of species i at age a+1 in year t+1 as a function of abundance at age a and year t.
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}} + N_{i,a+1,t}e^{-Z_{i,a+1,t}}$	Abundance of the plus group of species i at age $a+1$ in year t.
$F_{i,a,t} = s_{f_{i,a}}F_{i,t}$	Fishing mortality of species i at age a in year t.
$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}}e^{-Z_{i,a,t}}N_{i,a,t}.$	Commercial catch-at-age of species i at age a in year t.
$S_{i,a,t} = Q_i s_{s\,i,a} N_{i,a,t}$	Survey abundance-at-age of species i at age a in year t.
$Z_{i,a,t} = F_{i,a,t} + P_{i,a,t} + M_{0_i}$	Total mortality-at-age Z, the sum of fishing mortality, predation mortality, and residual natural mortality M_0.
Q_i	Survey catchability for species i.
$s_{f_{i,a}}$	Fishery selectivity-at-age for species i at age a
$s_{s_{i,a}}$	Survey selectivity-at-age for species i at age a
$F_{i,t}$	Full-recruitment fishing mortality for species i in year t.

Table 3A-2. Predation equations as per Van Kirk et al. [2010].

Equation	Description
$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_j \sum_b I_{j,b} N_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Predation mortality-at-age for prey species *i* at age *a* in year *t*.
$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Proportion of prey *i,a* in all food available to predator *j,b* in year *t*, assumed equal to the proportion of food within the stomach of predator *j,b* in year *t* composed of prey *i,a*.
$\phi_{i,a,j,b,t} = v_{i,a,j,b} B_{i,a,t}$	Biomass of prey *i,a*, in year *t* multiplied by a suitability coefficient *v*, which defines the probability of predator *j,b*, selecting for prey *i,a*.
$\phi_{j,b,t} = B_{oth} + \sum_i \sum_a v_{i,a,j,b,t} B_{i,a,t}$	Total food available in year *t* to predator *j,b*, defined as the sum of all available modeled prey plus a constant "Other Food" term which was set to e^{15}.
$v_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b}$	The product of species-preference ρ, and size-preference *g*. Size-preference *g* is temporally constant; species-preference can change relative to pooled stomach data.
$g_{i,a,j,b} = \exp\left[-\frac{1}{2\sigma_j^2} \left(\ln \frac{w_{j,b}}{w_{i,a}} - \eta_j \right)^2 \right]$	Size-preference function for predator *j,b*. Size-preference is constant over a variety of prey species, but *g* is prey-specific subscripted as prey species differ in size-at-age.

Table 3A-3. Objective function components as per Van Kirk et al. [2010]. A caret signifies model estimates.

Equation	Description
$\sum_i \sum_t \left[\ln(Ctot_{i,t} + 0.001) - \ln(\hat{C}tot + 0.001)\right]^2$	Total catch (lognormal)
$\sum_i \sum_t \left[\ln(Stot_{i,t} + 0.001) - \ln(\hat{S}tot + 0.001)\right]^2$	Total survey (lognormal)
$-\sum_i \sum_a \sum_t \left[\left(\frac{C_{i,a,t}}{Ctot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{C}_{i,a,t}}{\hat{C}tot_{i,t}} + 0.0001\right)\right]$	Catch-at-age (multinomial)
$-\sum_i \sum_a \sum_t \left[\left(\frac{S_{i,a,t}}{Stot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{S}_{i,a,t}}{\hat{S}tot_{i,t}} + 0.0001\right)\right]$	Survey-at-age (multinomial)
$\sum_i \sum_a \sum_j \sum_b \sum_t \left[\left(\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} + 0.0001\right) - \left(\frac{\hat{\phi}_{i,a,j,b,t}}{\hat{\phi}_{j,b,t}} + 0.0001\right)\right]^2$	Stomach-contents (normal)

CHAPTER 4

MULTISPECIES HARVEST CONTROL RULES AND BIOLOGICAL REFERENCE POINTS UNDER A MULTISPECIES AGE-STRUCTURED ASSESSMENT FRAMEWORK IN THE GULF OF ALASKA[1]

[1] K.F. Van Kirk, T.J.Quinn II, J.S. Collie, and Z.T. A'mar. Multispecies harvest control rules and biological reference points under a multispecies age-structured assessment framework in the Gulf of Alaska. In preparation to be submitted to the Canadian Journal of Fisheries and Aquatic Sciences

ABSTRACT

Fisheries models that explicitly include predation generally estimate higher prey abundances and different cohort dynamics than single-species constructs. This alters life-history parameters used to construct biological reference points (BRPs) upon which fisheries management is based. A multispecies age-structured assessment (MSASA) model for the Gulf of Alaska (GOA) was used to revise current BRPs in the GOA from a single-species into a multispecies context. Arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut *(Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*) were the modeled species. The performance of potential multispecies harvest control rules (HCRs) and management strategies was assessed through simulation work. Implementation of current control rules for pollock in the GOA using multispecies BRPs had higher risk of pollock spawning biomass decline than other HCRs. Reducing fishing pressure under conditions of increased pollock predation was practical, but these effects were limited under the simulation structure. Increasing fishing pressure on flounder to allow pollock increase was effective but impractical given halibut bycatch restrictions. Maximum sustained yield in this context will likely mean the default catch arising from multispecies BRPs and HCRs that satisfy management directives for all species in a given complex.

KEYWORDS: multispecies, predation, Gulf of Alaska, walleye pollock, arrowtooth flounder, Pacific cod, stock assessment, fisheries management

INTRODUCTION

The task of stock assessment scientists is to inform decision-making bodies regarding the condition of fish stocks and the probability of success in the implementation of various management strategies (Punt and Hilborn 1997); the goal is the sustainability of both fish abundances and the commercial yields taken from them (PFMC 1998). Potential management strategies are generally developed from simplified models of the stocks and systems under consideration in conjunction with various management goals (Punt and Smith 2001). The awareness that "...reality is often (substantially) outside the modeled estimates of uncertainty" (Punt and Smith 2001) has caused management bodies to recommend increasingly risk-averse criteria for setting catch levels as understanding of the natural variability in fish populations has grown (FAO 1995). The Magnuson-Stevens Act states "criteria used to set target catch levels should be explicitly risk-averse, so that greater uncertainty regarding status or productive capacity of a stock or stock complex corresponds to greater caution in setting target catch levels".

Fisheries scientists generally construct harvest control rules by means of biological reference points (BRPs), which serve to limit commercial harvest as a function of stock conditions (Garcia 1996). BRPs are estimated with various life-history parameters, including maturity-at-age, fishery selectivity, historical catch levels, estimates of spawner-recruit relationships or mean recruitment-at-age, and assumptions regarding natural mortality rates (Quinn and Deriso 1999). BRPs can be expressed as

acceptable rates of fishing mortality or minimum levels of spawning biomass and are updated as additional data become available regarding annual variations in a population (NRC 1998). The classic BRP is maximum sustainable yield (MSY), along with the associated spawning biomass that provides MSY to commercial fisheries while allowing for stock replenishment. Calculation of MSY, however, is difficult when the spawner-recruit relationship is uncertain, and proxies for MSY, as estimated from per-recruit studies, are often used instead, with $SB_{40\%}$ as a standard proxy for SB_{MSY} (Clark 1993, Quinn and Deriso 1999). For groundfish in Alaskan waters, the standard BRPs are estimates of $SB_{100\%}$, $SB_{40\%}$, and $F_{40\%}$. $SB_{100\%}$ refers to unfished female spawning biomass calculated from spawning biomass-per-recruit with full-recruitment fishing mortality $F = 0$, multiplied by mean annual recruitment over a given time period, $SB_{40\%}$ is simply $0.4*SB_{100\%}$, and $F_{40\%}$ is the full-recruitment fishing mortality that reduces $SB_{100\%}$ to $SB_{40\%}$. $F_{40\%}$ is regarded as a target mortality; there are also BRPs to define overfishing (a value for F), and overfished conditions (a value of SB) (PFMC, 2006).

Biological reference points are currently calculated from single-species stock assessments; these models often assume a constant known natural mortality (i.e., all mortality from factors other than the commercial fishery) across all ages for a given species. The majority, if not the totality, of natural mortality for non-apex species is composed of predation mortality (Gaichas et al. 2010). Predation mortality exceeds fishing mortality for many species (Bax 1998), is a primary driver of cohort structure for non-apex species (Van Kirk et al. 2012), and is highly variable over time relative to predator and prey abundances (Overholtz et al. 2008, Kinzey and Punt 2009). Models that

include predation show larger estimates of overall abundance for prey species than single species models (Jurado-Molina and Livingston 2002, Garrison and Link, 2004, Tyrell et al. 2008) and higher estimates of overall mortality (Hollowed et al. 2000, Tsou and Collie 2001, A'mar 2009). As these dynamics fundamentally alter the life-history parameters from which BRPs are calculated (Gislason 1999), the assumption of a constant natural mortality will produce inappropriate reference point estimates, affecting the efficacy of management strategies based upon them (Collie and Gislason 2001, Walters et al. 2005). Single-species stock assessments therefore potentially underestimate the risk associated with a given fishing strategy due to skewed estimates of life history parameters and underestimation of the connection strength between predator and prey species (Moustahfid et al. 2009, Tyrell et al. 2011).

Recognition of the role played in fish population dynamics by predation has resulted in a wide variety of multispecies models designed to integrate predation into stock assessment and trophic analyses (see Plagányi, 2007 for a review of various approaches and examples). As a result, management bodies and researchers have also recommended the development of multispecies BRPs and harvest control rules (HCRs) that reflect predation mortality and regulate fishing pressure accordingly (Gislason 1999, ICES 2008, Tyrell et al. 2011).

In this paper, we use a multispecies, age-structured assessment (MSASA) model (Van Kirk et al. 2010) for the Gulf of Alaska (GOA) to construct biological references points in a multispecies context, and assess the performance of potential harvest control rules and management strategies.

METHODS

MSASA Model Structure

The GOA MSASA model merges a number of single-species stock assessments via predation linkages into a unified multispecies model after the multispecies virtual population assessment (MSVPA) approach of Sparre (1980) and Pope (1979). The MSASA structure deviates from MSVPA methods in that diet data are assumed sampled with error, and stomach-contents are estimated from size- and species-preference functions and predator-prey relative abundances. Modeled species are arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumatopias jubatus*). Fig. 4.1 shows predation linkages between species. Parameter estimates are obtained via maximum likelihood methods in AD Model Builder (Fournier et al. 2011). Catch, survey, and stomach-content datasets for model fitting are taken from are taken from the Alaska Fisheries Science Center (AFSC) Stock Assessment and Fishery Evaluation (SAFE) reports and the Resource Ecology and Ecosystem Modeling (REEM) database of the AFSC from 1981 – 2001 (Table 4.1). Sampled stomach-contents were pooled into three periods to compensate for data scarcity; species-preference parameters were estimated for each period to reflect changes in predator selection relative to changes in predator-prey abundances. Annual recruitment at age 1, catch, survey

abundance, and mortalities from commercial fishing, predation, and residual natural mortality M_0 were estimated for pollock, cod, and flounder. Abundances-at-age for apex predators Steller sea lion and Pacific halibut were input, as were annual rations.

Estimates of total annual predation mortality-at-age for pollock, flounder and cod from the GOA MSASA model are presented in Figure 4.2. A complete description of model structure and analyses of results is given in Van Kirk et al. (2010, 2012); model equations are summarized in Appendix 4A.

Single-species and Multi-species Context

The GOA MSASA model can be reverted to three single-species models by simply replacing the sum of predation mortality and residual natural mortality with the constant values for natural mortality M used in AFSC stock assessments for flounder, cod, and pollock. Comparison between the two demonstrates some of the points discussed above regarding the difference between single-species and multispecies contexts. The multispecies model showed higher abundances for flounder and pollock than the single-species approach (Fig. 4.3), as those species incur heavy predation mortality, while abundances for cod were similar between the two approaches given low predation rates on them (Fig. 4.3). Age-specific predation mortality also affects spawning abundance and biomass per recruit. These factors alter estimates of $F_{40\%}$ and spawning biomass per recruit, even though estimates of $SB_{100\%}$ remain similar (Table 4.2).

The significant predation on flounder and pollock occurs on younger ages prior to full recruitment into the commercial fishery. In contrast, predation on cod is much lower and focused primarily on ages 6 – 9 which are subject to full-recruitment *F*. Accordingly, values of yield-per-recruit conditioned on mean predation mortality-at-age for ages 5+ as a function of full-recruitment fishing mortality *F* are higher for pollock and flounder in the multispecies context, given the need for additional prey biomass to meet the demands of predation (Fig. 4.4). The slope of the decline in yield-per-recruit is dependent on both commercial fisheries gear selectivity and size-preference on the part of the modeled predators. Predation mortality on cod is focused mostly on ages 6 – 9 (Fig. 4.2), and the highest age-specific yield is from age 5, meaning that little if any decline in yield-per-recruit as a function of *F* is seen in Fig. 4.4. Pollock and flounder, however, are both subject to fisheries removals and predation mortalities at ages younger than 5, and the resulting decline in yield-per-recruit is sharper than for cod. It is important for fisheries managers and decision-making bodies to understand that the apparent increase in abundance and potential yield-per-recruit when these species are modeled in a multispecies context does not imply increased fishing pressure on the modeled species, as the biomass should not be considered an increase of surplus production, but a separate category relegated to the necessities of the system population dynamics (Collie and Delong 1999). Figure 4.4 is also an approximation using mean predation values– a true multispecies yield-per-recruit also varies relative to variations in predation mortality-at-age. Given that predation mortality varies relative to fishing pressure on both predators and prey, conceptualizing such a multidimensional complex surface becomes difficult.

Biological Reference Points and Harvest Control Rules

Since 1997, the North Pacific Fisheries Management Council (NPFMC) has managed stocks under its jurisdiction by a series of tier rules governing fishing pressure. All three modeled prey species (cod, pollock, and flounder) currently fall under Tier 3, which is predicated on the ratio of annual spawning biomass to estimates of $SB_{40\%}$, the target value of spawning biomass. The following harvest control rules govern species with Tier 3 designation:

$$F_{ABC} \leq \begin{cases} F_{40\%} & \text{if } SB/SB_{40\%} > 1 \\ F_{40\%}[(SB/SB_{40\%} - \alpha)/(1-\alpha)] & \text{if } \alpha < SB/SB_{40\%} \leq 1 \\ 0 & \text{if } SB/SB_{40\%} \leq \alpha \end{cases} \tag{4.1}$$

for which $\alpha = 0.05$ is the relative biomass threshold below which no fishing is allowed, F_{ABC} = the fishing mortality producing the acceptable biological catch (ABC), resulting in progression to the target $SB4_{0\%}$. These quantities ($F_{40\%}$, $SB_{40\%}$, etc.) are known as biological reference points (BRPs). There is also a limiting fishing mortality, F_{OFL}, that results in overfishing, which would result in a yield denoted as OFL for "overfishing level". In this paper, we only evaluate target HCRs for simplicity.

These guidelines are intended to provide a buffer between ABC and OFL in the face of uncertainty surrounding estimates of spawning biomass from stock assessment efforts. Dorn et al. (2001) proposed a more conservative approach to maintaining the buffer between F_{ABC} and F_{OFL} for GOA pollock as

$$Define: SB^* = SB_{40\%} \frac{F_{35\%}}{F_{40\%}}$$

(4.2)

$$Stock\ Status:\ SB / SB^* > 1,\ then\ F = F_{40\%}$$

$$Stock\ Status:\ 0.05 < SB / SB^* \leq 1\ ,\ then\ F = F_{40\%}\ (SB / SB^* - 0.05) / (1-0.05)$$

$$Stock\ Status:\ SB / SB^* \leq 0.05,\ then\ F = 0.$$

Multispecies BRPs and HCRs are intended to regulate fishing pressure in light of the potential consequences that fishery removals of one species may have on those linked to it through predation, and to provide a buffer between fishing pressure and uncertainty in assessment of target populations due to predation mortalities. To examine the development of multispecies BRPs and HCRs, we constructed a set of simulations, conditioned on parameter and population estimates from the fitted GOA MSASA model. Various single-species and multispecies HCRs were evaluated. We first removed fishing mortality from the simulation to obtain an unfished baseline, and then assessed changes to the system when various HCRs are implemented.

Simulation Structure

We used parameter estimates from the fitted model and assumed that other potential sources of uncertainty remained constant. These simulations were not intended to be true "forward projections" extrapolating abundance trends specifically from 2010 conditions, but rather a general examination of system dynamics under varying conditions and the potential efficacy of the implemented management strategies.

The basic structure of the simulation models was the same as the fitted GOA MSASA model, projecting multispecies dynamics over 50 years, starting from year 2010. A summary of population structures and statistical distributions is presented in Table 4.3, all of which were conditioned on model outputs and data.

Annual Recruitment

The AFSC stock assessments do not use spawner-recruit relationships for the modeled species due to uncertainty (Dorn et al. 2011, Thompson et al. 2010, Turnock and Wilderbuer, 2011). Annual recruitment at age-1 for fish species was therefore assumed to vary normally around mean log-recruitment. Variances for random draws were estimated from species-specific recruitment over all fitted model years (Table 4.3). Mean annual pupping rate for sea lions was taken from Winship et al. (2002) under the assumption of a stable population.

Mortality

Mean residual natural mortalities M_0 for flounder, cod and pollock were set to fitted model estimates (Table 4.3). Variability in age-specific total mortality for each year was the outcome of changes in predation mortality; M_0 values remained constant. Sea lion survival rates for each age were gender-specific means taken initially from Winship et al. (2002), modified for use in the MSASA model structure, and implemented here

along with pupping rates to produce a stable population. Mean total mortality for Pacific halibut was estimated by fitting an exponential decline to observed abundances-at-age from 1981 – 2010 (Table 4.3).

Predation Components

Size-preference parameters for the predation function were set to fitted model means and remained constant. Species-preference parameters were allowed to vary every five years as a random walk in which the step size was proportional to the mean change observed in species-preference parameters over the fitted model periods. Random draws from uniform distributions between 0 and 1 were used to direct step direction: if the random draw was less than 0.33, the step was negative; if between 0.33 and 0.66, the parameter did not change; if greater than 0.66, the step direction was positive.

Stock Condition Indicators

Spawning biomass for a given species in year t was defined as

$$SB_t = \sum_{a=1}^{x} m_a w_a N_{F_{t,a}} \tag{4.3}$$

for which m_a is the proportion mature at age a, w_a is the weight at age a, and $N_{Ft,a}$ is the abundance of females of age a in year t. For cod and pollock, female abundance was

assumed to be 50% of total abundance; for flounder, females were assumed to be 70% of the population (Turnock and Wilderbuer 2011).

Simulation Configurations

We present five simulations designed to assess multispecies population dynamics in the Gulf of Alaska under a variety of potential applications starting with the conservative HCR in (4.2). We focused primarily on pollock dynamics in terms of evaluating the efficacy of potential management strategies, as pollock have a complete predator profile in the GOA MSASA fitted model (i.e., $M_0 = 0$). Each simulation projected population dynamics over 50 years, and each simulation was replicated 1000 times. No parameter estimation was implemented – calculations were all based on fitted model parameter values.

BRP 0. $F = 0$. Population dynamics were assessed in the absence of fishing mortality.

BRP 1. $F = F_{ABC}$. For pollock and cod, full-recruitment fishing mortality F was set to the level defined by eq. (4.2) using the single-species BRPs with estimated parameters from the GOA MSASA fitted model in a single-species context (Table 4.2). Flounder fishing mortality in the GOA has generally been far below F_{ABC} levels; while the 2010 F_{ABC} was 0.183, the actual F level was calculated to be 0.019 (Dorn et al. 2011). Following this disparity between allowable and implemented catch levels, we set flounder F_{ABC} to be constant at 10% of the calculated $F_{40\%}$, at 0.035.

BRP 2. As in BRP 1, except that the BRPs were taken from the GOA MSASA model in a multispecies context (i.e., with predation) (Table 4.2), with flounder F proportionally reduced as in BRP 1.

BRP 3. As in BRP 2, with the exception that SB^* for pollock was adjusted upwards (reducing fishing pressure) when predation mortality on pollock exceeded median values from the unfished system in BRP 0. As a potential management strategy, we proposed a correction factor to compensate for increased levels of predation mortality from flounder on age 1 pollock, and from cod on age 5. Flounder feed heavily on younger pollock, whereas cod predation is highest on intermediate ages. Predation on the earliest ages has the potential to result in drastic declines in overall prey abundance; predation on age 5 pollock removes fish at the point of 50% maturity, reducing the number of individuals entering reproductive maturity and thereby limiting spawning biomass. Age five is also the youngest age at which full recruitment into the pollock commercial fishery was estimated to occur in the GOA MSASA model. Five year-old pollock therefore represent a potential bottleneck for spawning biomass, subject to full-recruitment fishing pressure in conjunction with cod predation at the same time the fish are entering reproductive maturity. The correction factor was implemented when predation on age 1 pollock from flounder and/or cod on age 5 pollock from cod exceeded their respective median levels from BRP 0 as

$$SB_{\text{mod}} = SB^* \left(\frac{p_t}{p_{median}} \right) \tag{4.4}$$

for which p_{median} is the appropriate median predation mortality from BRP 0 and p_t is the level of predation mortality in model year t. The median was selected over the mean to provide more stability in the HCR. Increases in SB^* were capped when $SB_{mod} = SB_{100\%}$ (Fig. 4.5). The implemented HCR, in which SB_{ref} represents the target pollock spawning biomass below which fishing pressure is reduced as per eq. (4.2), is therefore

$$SB_{ref} = \begin{cases} SB^* & \text{if } p_t \le p_{median} \\ SB_{\text{mod}} & \text{if } p_t > p_{median} \\ SB_{100\%} & \text{if } SB_{\text{mod}} > SB_{100\%} \end{cases} \tag{4.5}$$

BRP 4. As in BRP 3, with the exception that instead of lowering pollock fishing pressure to compensate for increased predation mortality as in BRP 3, we experimented with raising full-recruitment fishing mortality F for arrowtooth flounder to reduce predator levels and allow prey recovery. We raised flounder F to $F_{40\%}$ level (Table 4.2; $F_{40\%} = 0.35$) and implemented a correction factor when predation mortality on age 1 pollock from flounder in a given year t rose above the median levels from BRP 0 as

$$F_{\text{mod}} = F_{40\%} * \left(1 + \left(\frac{p_t}{p_{median}} - 1\right) * 5\right), \tag{4.6}$$

with the implemented HCR given by

$$F = \begin{cases} F_{40\%} & \text{if } p_t <= p_{median} \\ F_{\text{mod}} & \text{if } p_t > p_{median} \end{cases} \tag{4.7}$$

For BRP 4 we considered such a strategy only between flounder and pollock, as cod are already fished close to F_{ABC}, and a management strategy that included raising those levels

was considered infeasible. The curves for alterations to pollock SB^* and flounder F from eqs. (4.4 – 4.7) are presented in Figure 4.5.

We also did not implement a management strategy like either BRP 3 or BRP 4 to pollock cannibalism on age 1 pollock; the feedback loop and lack of spawner-recruit relationship relative to density-dependence precluded accurate assessment of such dynamics. A summary of each simulation configuration is presented in Table 4.4.

RESULTS

Spawning biomass equilibrium for all three species was reached after an initial "burn-in" period of roughly ten years (Fig. 4.6). Pollock and cod spawning biomass were significantly below BRP 0 levels in all fished systems (BRP 1 - 4), as expected. Spawning biomass levels were lowest for pollock in BRP 1, slightly higher in BRP 2, roughly equivalent to $SB_{40\%}$ in BRP 3, and above $SB_{40\%}$ in BRP 4. For cod, spawning biomass levels were virtually equivalent in BRP 1 – 4. Flounder SB levels were increased from BRP 0 in BRP 1 - 3, but showed a marked drop in BRP 4 to below $SB_{40\%}$ levels, as was designed. Variability in spawning biomass projections for pollock and cod was lower under fished simulations (BRP 1 - 4) than unfished simulations (BRP 0), although variability in flounder spawning biomass showed marked reduction only in BRP 4 (Fig. 4.6).

BRP 0 showed the lowest proportion from all cases of pollock and cod spawning biomass estimates falling below $SB_{40\%}$ (Fig. 4.7). For BRP 1 - 4, BRP 1 had the highest

proportion of pollock *SB* estimates below $SB_{40\%}$, while for cod, BRPs 2 - 4 were nearly the same, and BRP 1 showed a slightly lower probability of $SB < SB_{40\%}$ (Fig. 4.7). BRP 0 estimates of flounder *SB* showed a slightly higher probability of falling below $SB_{40\%}$ than BRP 1 - 3, with the probability of $SB < SB_{40\%}$ significantly higher in BRP 4 than any other (Fig. 4.7). For pollock, the probability of *SB* falling below $SB_{20\%}$ was highest for BRP 1, while for flounder, it was BRP 4; cod SB levels did not fall below $SB_{20\%}$ under any BRP (Fig. 4.7).

Median full recruitment fishing mortality *F* was assessed for years 11 – 50 to eliminate the higher variability during initial "burn in" during years 1 – 10 (Fig. 4.8). Pollock *F* varied between BRPs; the highest *F* values were for BRP 4, at roughly 0.35, with BRPs 1 – 3 showing relatively similar levels (0.18 to 0.28). Median cod *F* values were nearly identical for BRPs 2 – 4, hovering around 0.52 and dropping to roughly 0.36 in BRP 1. Values for flounder *F* remained set at 0.035 for BRPs 2 – 4 and only varied in BRP 4, for which they ranged between 0.35 and 0.55.

Median annual total catch levels for pollock in BRP 1 - 3 were below mean total annual catch levels from 1981 – 2010 from the AFSC stock assessments; catch levels in BRP 4 were roughly twice mean AFSC levels (Fig. 4.9). Median annual total catch levels for cod exceeded 1981 – 2010 mean catch levels for all cases, with BRP 1 showing the lowest catch levels (Fig. 4.9). Median annual total catch levels for flounder exceeded mean 1981 – 2010 levels for all cases, with BRP 4 producing flounder catch levels 1000% higher than the other fished simulations (Fig 4.9).

Mean predation-at-age on pollock remained generally stable across all BRPs (Fig. 4.10). As expected, predation from flounder fell in BRP 4, and predation from Steller sea lions on ages 8 – 10 rose slightly under fished conditions (BRPs 1 - 4). Predation from cod on ages 5 – 10 in BRP 0 was higher than in other cases, and cod predation on flounder was higher for flounder ages 7 – 14 in BRP 0 (Fig. 4.11a). (Cod predation on age 15 flounder was very low due to very narrow size-preference distributions for cod as predator, estimated by the 1981 – 2010 GOA MSASA model.) Examination of all BRPs showed that the absolute biomass of flounder aged 7 – 14 consumed by cod was higher in the unfished case (Fig. 4.11b). Analysis of estimated cod stomach contents and size-preferences produced by the fitted GOA MSASA model, which were used to define cod preferences and feeding behavior in the simulations, showed that the ages of cod feeding on flounder ages 7 – 14 were exactly the ages fully recruited into the commercial fishery (Fig 4.11c).

DISCUSSION

The results strongly suggest that a management strategy of "fishing down" a target predator to allow for increases in prey abundance (BRP 4) is highly effective. Moreover, these results imply that commercial fishery operations in the Gulf of Alaska have already altered the multispecies equilibrium. By reducing cod ages 5 – 12, predation mortality on flounder ages 7 – 14 is reduced, producing higher flounder abundance, as in BRP 2 – 4 relative to BRP 0 (Fig. 4.6). In terms of the observed increase of arrowtooth

flounder in the GOA since the early 1980s and the attendant decline of pollock, it may very well be that the commercial cod fishery itself has contributed to the very situation for which potential solutions are now being sought.

Although BRP 4 was the most effective of the examined management strategies, with catch levels for cod above historical means and pollock yield only slightly below (Fig. 4.8), and the lowest risk of pollock decline (Fig. 4.7), fishing down flounder in the Gulf of Alaska is unlikely to be a practical approach to increasing the abundance of pollock. Flounder commercial fisheries operations are currently limited by restrictions on the bycatch of Pacific halibut, preventing large increases in fishing pressure on flounder.

The results also point out the risk of using single-species BRPs and harvest control rules when strong predator-prey linkages exist between the managed species. The buffer between fluctuations in spawning biomass and commercial fisheries removals that might inadvertently drop *SB* levels below benchmarks is reduced under these conditions. Of the BRPs examined, BRP 1 showed the highest risk of pollock *SB* falling below both $SB_{40\%}$ and $SB_{20\%}$, suggesting that pollock *SB* falling below $SB_{20\%}$ and thereby closing the commercial fishery is possible.

Only when conditioned on biological reference points estimated from a multispecies context (Table 4.2) did implementation of the current single-species harvest control rules in the Gulf of Alaska (BRP 2) appear to be a moderately practical method for multispecies management. This suggests that using $SB_{40\%}$ as a proxy for SB_{MSY} for pollock in the GOA is potentially robust to stock variability arising from predation and

predator abundances. The risk of *SB* falling below $SB_{40\%}$ for cod and pollock should be examined by NPFMC to assure that greater protection for pollock is not necessary.

BRP 3 produced pollock *SB* levels consistently close to $SB_{40\%}$ (Fig. 4.6) and a lower probability of pollock decline than BRP1 or BRP2 (Fig. 4.7), but the dynamics of this strategy are poorly represented in the current model structure. The change in predator-to-prey ratios between BRP 0 and BRP 3 suggests that reducing fishing pressure in the face of high predation on age 5 pollock resulted in greater increases to spawning biomass than reduction in *F* due to high levels of flounder preying on age 1 pollock. The lack of a spawner-recruit function, however, prevented the increase in age 5 pollock from contributing to increased recruitment, which could potentially be an important feedback loop for increasing prey abundance. Age-1 pollock are not targeted by the commercial fishery; reduction in *F* levels in response to predator abundance was intended to allow greater passage of age-1 biomass through ages 2 – 5 to contribute to spawning biomass, but any increase in younger cohorts was apparently simply consumed by unchanged flounder abundances. As the increase in pollock spawning biomass was due only to reduced fishing mortality on age 5 fish, this approach should be revisited when a robust spawner-recruit function is available. The loop of increased spawning biomass and the attendant increase in age-1 recruitment to meet predation needs that would then increase the strength of the cohort entering age 5 could potentially prove a highly effective mechanism for rebuilding depleted fish stocks.

This lack of spawner-recruit relationships in the Gulf of Alaska presents an obstacle to assessing population dynamics. As expected, catch and spawning biomass

appeared moderately correlated in BRPs 1 - 4 on general principle, but without spawner-recruit curves the strength of this correlation is weakened. The assumption that spawning biomass and recruitment are independent resulted in consistent recruitment levels over time regardless of impacts to spawning biomass from predation or fishery removals. Using mean recruitment determined under fished conditions (i.e. from the fitted 1981 – 2010 GOA MSASA model) meant that the simulations could not incorporate potentially increased recruitment under unfished conditions arising from the combination of increased spawning biomass and an accurate spawner-recruit curve (NMFS 2002). The result was that recruitment was unaffected by cessation of commercial fisheries operations (BRP 0), and the only changes in an unfished system were predation mortality and the survival of individuals normally removed in the fishery. Halting commercial fisheries in the GOA would most likely produce far more complex results. In other simulation work, $SB_{100\%}$ and SB_{MSY} were more responsive to perturbations with better results when a spawner-recruit function was available (Haltuch et al. 2008).

Multispecies harvest control rules must balance the spawning biomass levels necessary to sustain target populations with socio-economic pressures; commercial catch cannot go to zero, but a multispecies approach to management might necessitate changes to ideas of acceptable harvest levels. Although multispecies MSY levels may be different than single-species MSY, neither cod nor pollock has been overfished in the Gulf of Alaska, suggesting that mean historical $F < F_{MSY}$ and that current management strategies based on single-species models are providing sustainable catch levels. While it is likely that uncertainty in stock assessments relative to predation mortality is underestimated

through the use of a constant natural mortality *M*, the implication is that current fisheries removals in the GOA are more sustainable than not and can provide significant information towards the development of multispecies management, provided that the context in which they are understood is improved through the implementation of multispecies models.

Maximum sustainable yield (MSY) also has different implications in this context regarding the surplus production available for commercial removals. Initially a target of managers, MSY purported to be the precise amount of surplus production capable of being removed from a given species on an annual basis that would maximize commercial yield while allowing stock perpetuation (Punt and Smith 2001). Criticism of MSY from mathematical, economic, and management perspectives has cast doubt upon its validity as a dependable management paradigm (Larkin 1977), but instead of disappearing, the concept has shifted from a target to a threshold or limit to be avoided. Conservative harvest control rules have been developed that account for uncertainty in stock assessments and variability in ecosystem processes (Mace 2001, Punt and Smith 2001). The difficulty of defining MSY for multiple species simultaneously has been recognized (ICES 2008). Mueter and Megrey (2006) and Pope (1976) concluded that overall surplus production available for commercial removal was less than a simple aggregate of surplus-production estimates from single-species assessments, while Brander and Mohn (1991) showed that such a conclusion is inherently dependent on the methods by which predation equations are implemented, and that a multispecies MSY is not necessarily less than a single-species aggregate.

In discussing MSY, the Pacific Fisheries Management Council stated "...consequently, it will be difficult if not impossible to obtain F_{MSY} and the biomass that produces MSY (i.e. B_{MSY}) for several species simultaneously" (PFMC 1998). Selection of one or two primary species and their associated BRPs within a given region may, by virtue of predation linkages and restrictions on other species connected by them, automatically establish catch levels and default management criteria. In terms of the cod-flounder-pollock interactions in this study, it could be asserted that the cod fishery should be limited to allow for greater predation on flounder. Maximum productivity for flounder is not a desirable management goal, given lack of market and the resulting consumption of pollock spawning biomass. By selection of the target fishery (pollock and cod), the attendant restrictions on a complex system may well produce a limited set of management options. In this context, MSY may evolve to mean simply a management strategy that is tolerable to stakeholder demands for all important species in the complex.

The second and third-order effects observed between the cod fishery, flounder abundances, and predation on pollock emphasize the need for including complex dynamics between modeled species, especially when a species functions as both predator and prey, when attempting to define multispecies dynamics and management strategies based upon them. Multispecies models incorporating uni-directional predation on a single prey species miss these dynamics and potentially draw erroneous conclusions regarding harvest control rules (Punt and Leslie 1995). The GOA MSASA model includes all major pollock predators, but is limited regarding cod and flounder predators and the potential linkages that could affect fisheries management. Beyond a certain point, however, model

expansion and the inclusion of additional species results in severe instability and excessive variances in parameter estimation, and the use of multiple "minimal realistic models" (Punt and Butterworth 1995) has been shown more effective than endless expansion (Fulton et al. 2003).

This study evaluates general multispecies dynamics as evidenced by GOA species and relationships, and as such should be applicable to other species and locations. Using mean values from the GOA MSASA fitted model, keeping species-preference constant, and ignoring other sources of stochastic uncertainty most likely produced overly simplistic results. The changes to pollock spawning biomass and the interactions of predator and prey species under the examined harvest control rules should therefore be considered relative to the unfished equilibrium of BRP 0, as opposed to strict absolute values applicable to the Gulf of Alaska. All four management strategies (BRPs 1 - 4), however, should prove applicable to a variety of systems under various conditions and constraints and aid in the continued development of practical multispecies fisheries management.

ACKNOWLEDGMENTS

This work was funded by the Pollock Conservation Cooperative Research Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Alaska. However, the findings and conclusions presented by the authors are their own

and do not necessarily reflect the views or positions of the Center or the University of Alaska.

This publication is also the result of research sponsored by Alaska Sea Grant with funds provided by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project no. R/31-11, 14), and from the University of Alaska with funds appropriated from the State.

This publication is also the result in part of research and education sponsored by the Cooperative Institute for Arctic Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreement NA17RJ1224 with the University of Alaska.

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Table 4.1. Catch and survey data from ASFC stock assessments used in fitting the 1981 – 2010 GOA MSASA model.

Data	Years Available	SAFE Table
Flounder total annual catch	1981 - 2010	Turnock and Wilderbuer 2009, Table 7.1
Cod total annual catch	1981 - 2010	Thompson et al. 2010, Table 2.1a
Pollock total annual catch	1981 - 2010	Dorn et al. 2011 Table 1.1
Flounder survey biomass	Tri-annually: 1984 - 2009	Turnock and Wilderbuer 2009, Table 7.3
Cod survey biomass	Tri-annually: 1984 - 2009	Thompson et al. 2010 Table 2.11
Pollock survey biomass	Tri-annually: 1984 - 2009	Dorn et al. 2011 Table 1.7
Flounder survey-at-age	Tri-annually: 1984 - 2009	Turnock and Wilderbuer 2009, Table 7.5
Cod survey-at-age	Tri-annually: 1984 - 2009	Thompson et al. 2010 Table 2.9a
Pollock survey-at-age	Tri-annually: 1984 - 2009	Dorn et al. 2011 Table 1.9
Cod commercial catch at age	1981 - 2010	Thompson et al. 2011 Tables 2.6a – 2.8b
Pollock commercial catch at age	1981 - 2010	Dorn et al. 2011 Table 1.5

Table 4.2. Estimates of SB100%, SB40%, F40%, recruitment, and spawning biomass-per-recruit (SPR) from the fitted 1981 – 2010 GOA MSASA model in both single-species and multi-species contexts; the AFSC stock assessments assess flounder recruitment at age 3, cod at age 1, and pollock at age 2.

Species	Source	*Recruits millions*	*SPR (F=0) (kg/rcrt)*	$SB_{100\%}$ *(1000 tons)*	$SPR_{40\%}$ *(kg/rcrt)*	$SB_{40\%}$	$F_{40\%}$
Pollock	SINGLE	941 (age 2)	0.789	743	0.319	300	0.38
	MULTI	2091 (age 2)	0.344	719	0.137	287	0.35
Cod	SINGLE	250 (age 1)	1.404	352	0.569	161	0.50
	MULTI	251 (age 1)	1.253	314	0.504	127	0.67
Flounder	SINGLE	515 (age 3)	1.953	1006	0.790	407	0.29
	MULTI	3121 (age 3)	0.322	1044	0.132	414	0.35

Table 4.3. Summary of simulation conditions for BRP 1 - 4.

Variable	Frequency	Conditions and values
Flounder recruitment	Annually	LN ~ (16.636, 1.651)
Cod recruitment	Annually	LN ~ (12.198, 0.389)
Pollock recruitment	Annually	LN ~ (16.282, 0.221)
Halibut recruitment	Annually	LN ~ (9.201, 0.121)
Sea lion pupping rate	Annually	0.22*total adult abundance
Flounder residual mortality	Constant	0.26
Cod residual mortality	Constant	0.35
Pollock residual mortality	Constant	0.00
Halibut total mortality	Constant	0.27
Sea lion survival at age	Time and age-constant	From Winship et al. (2001)
Size-preference coefficients	Constant	Set to mean MSASA model estimates
Species-preference coefficients	Constant	Random-walk every five years

Table 4.4. Summary of the harvest control rules implemented for BRP 1 - 4.

Simulation	Conditioning
BRP 0	$F = 0$
BRP 1	F = single-species F_{ABC} for all pollock and cod as per eq. (4.5). Flounder $F_{ABC} = 0.035$; cod $F_{ABC} = 0.5$; pollock $F_{ABC} = 0.37$.
BRP 2	F = multi-species F_{ABC} for all pollock and cod as per eq. (4.5). Flounder $F_{ABC} = 0.035$; cod $F_{ABC} = 0.65$; pollock $F_{ABC} = 0.35$.
BRP 3	Pollock F reduced when predation from flounder on age 1 pollock and/or predation from cod on age 5 pollock exceeded median levels from BRP 0. Eq. (9).
BRP 4	Flounder F increased when predation from flounder on age 1 pollock exceeded median levels from BRP 0. Eq. (10).

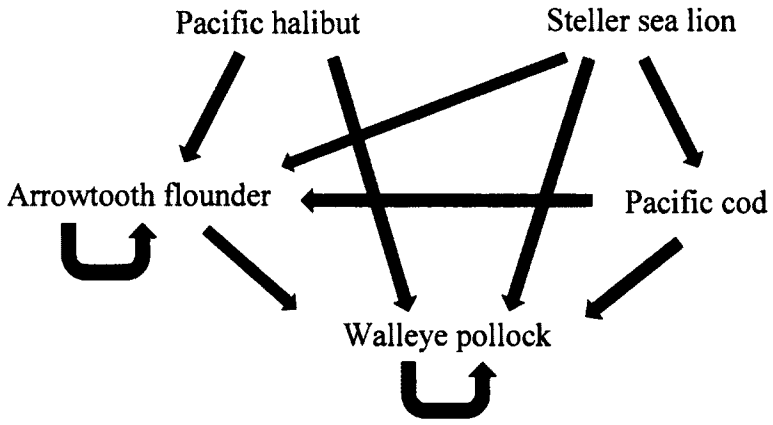

Figure 4.1. Predation linkages in the GOA MSASA model as per Van Kirk et al. (2012); curved arrows indicate cannibalism.

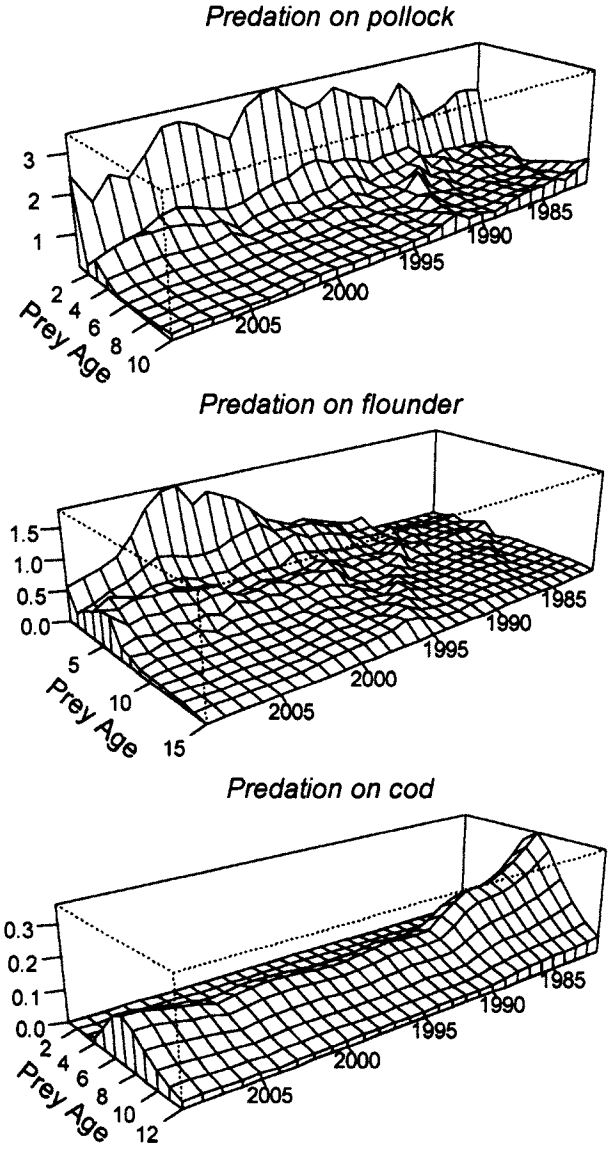

Figure 4.2. Total annual predation mortality-at-age estimated by the GOA MSASA fitted model from 1981 – 2010 for pollock, flounder, and cod.

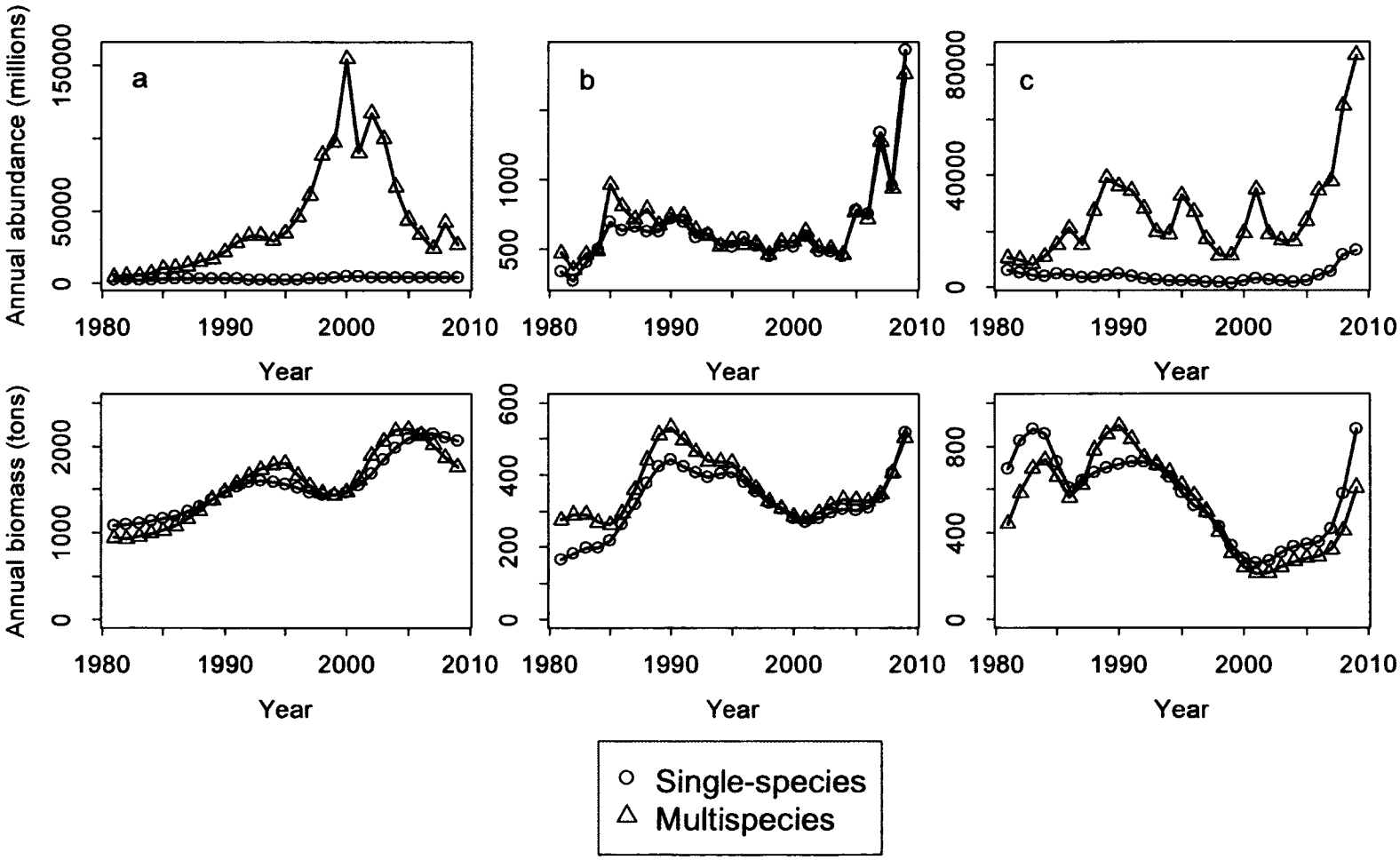

Figure 4.3. Total annual abundance and biomass for (a) flounder, (b) cod, and (c) pollock from the GOA MSASA model structures assessed under single-species and multispecies conditions.

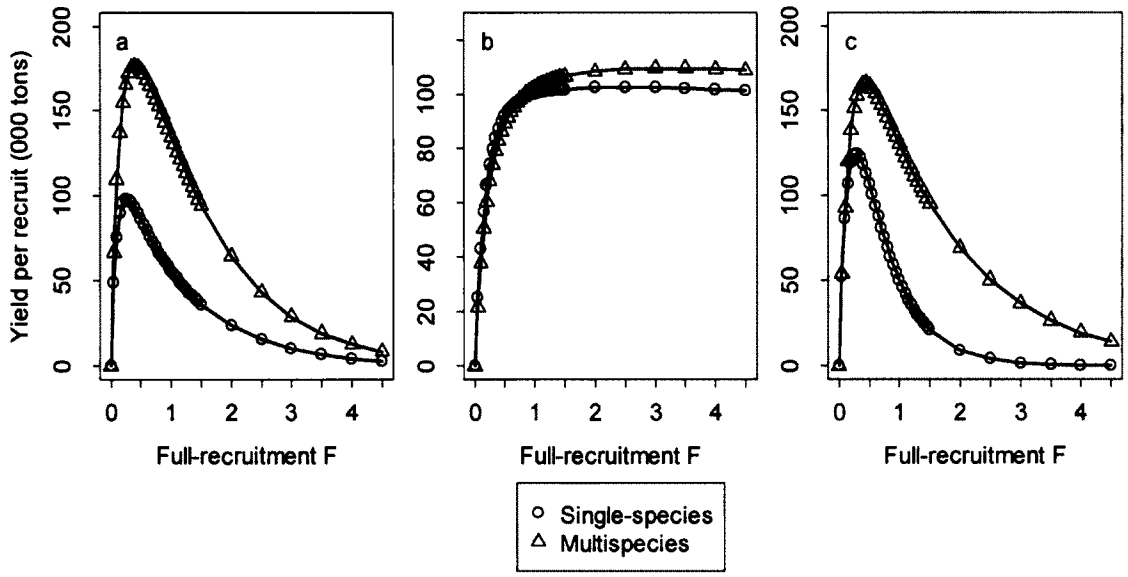

Figure 4.4. Yield-per-recruit for (a) flounder, (b) cod, and (c) pollock comparing a single-species to a multi-species context, for which the single-species output was from the GOA MSASA fitted model run without predation and with M set to AFSC stock assessment values.

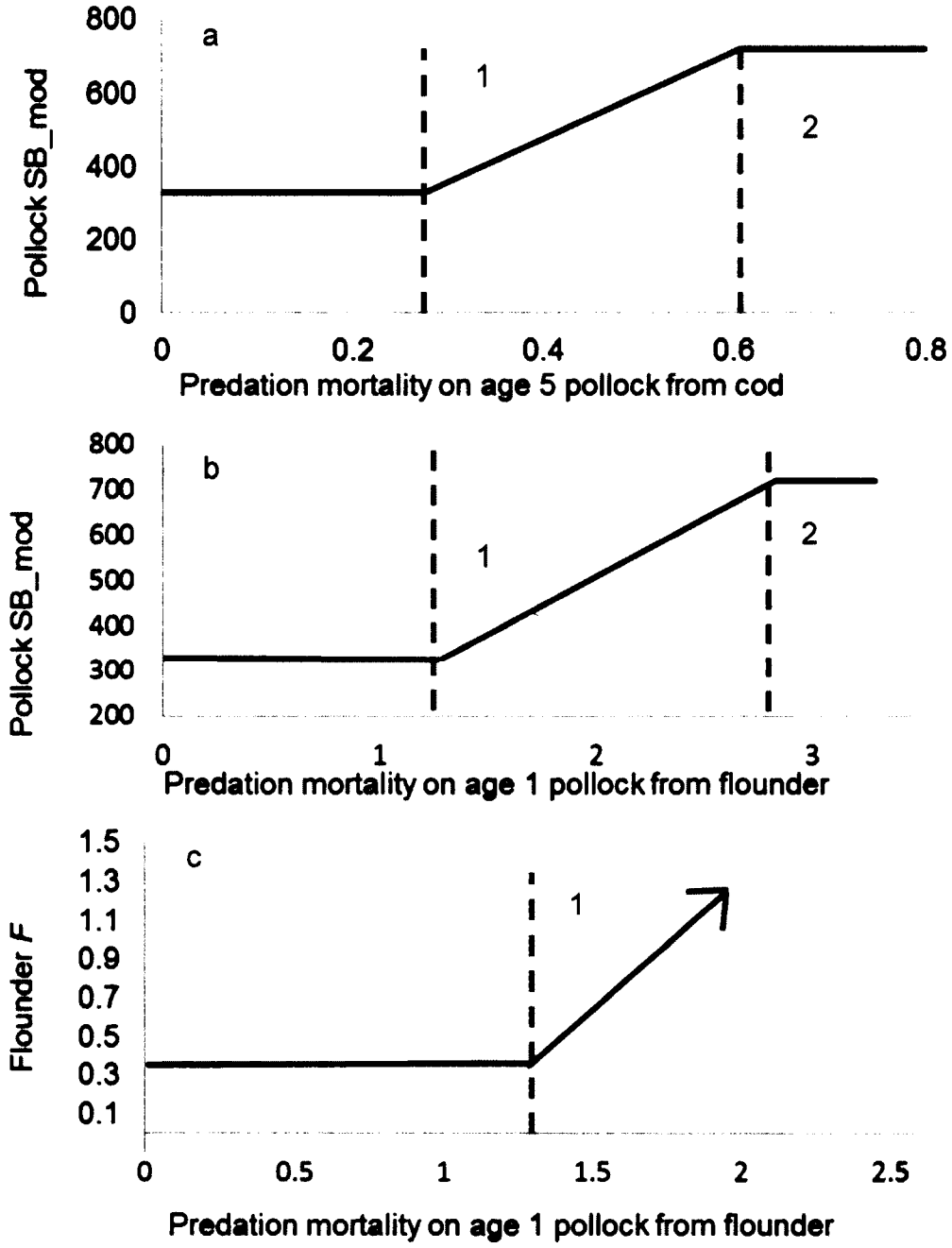

Figure 4.5. Modifications to pollock SB* and flounder F – (a) increase in pollock SB* relative to increases in the ratio of cod predators to age 5 pollock in BRP 4; (b) increase in pollock SB* relative to decreases in the ratio of age 1 pollock to flounder predators in BRP 4; (c) reduction in full recruitment flounder F relative to increases in flounder predators on age 1 pollock in BRP 5. Dashed line (1) = median predation mortality from BRP 0, at which point increases in SB* or F are incurred; dashed line (2) = point at which SB* = SB100%.

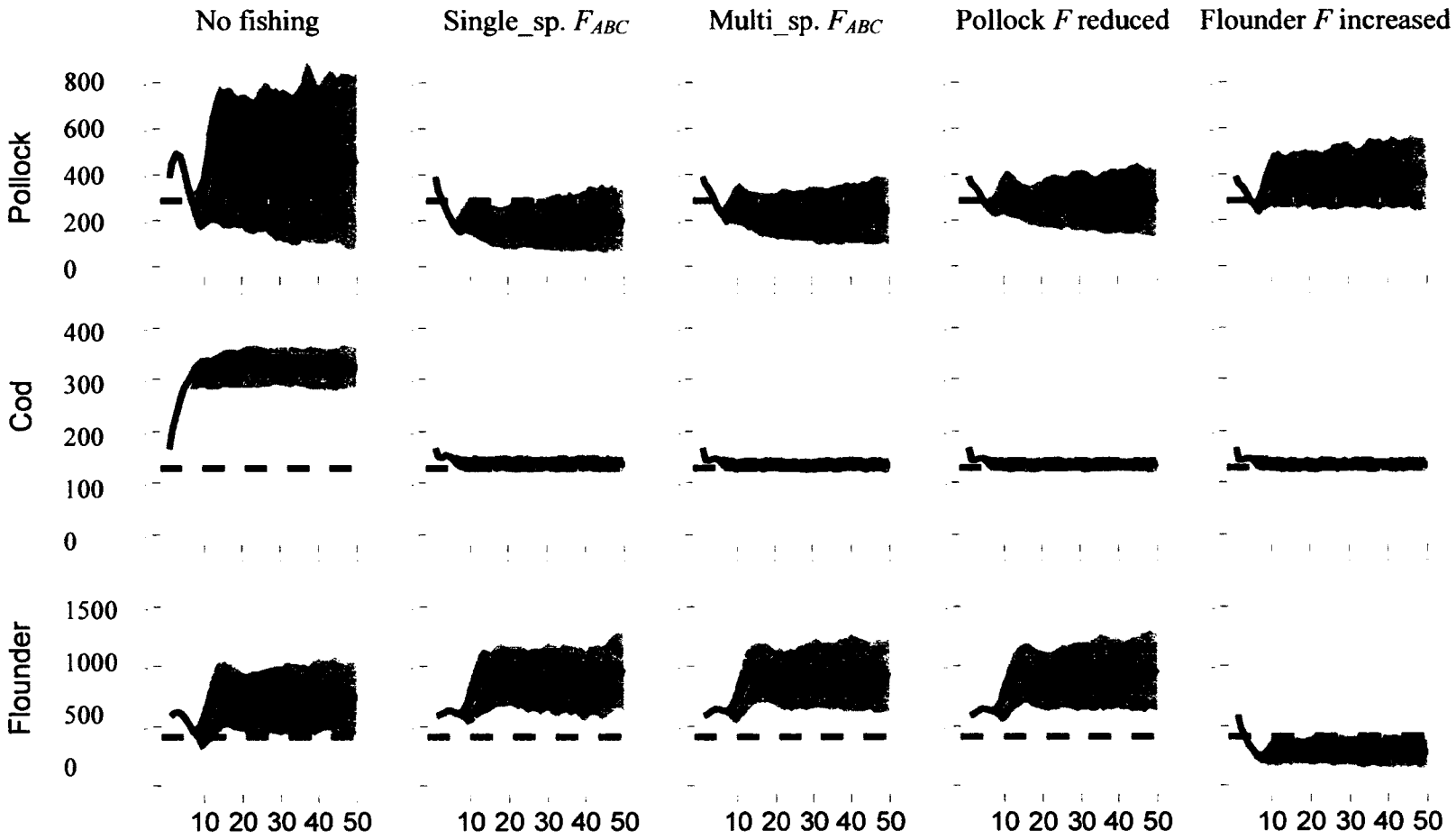

Figure 4.6. Median spawning biomass in tons (solid lines) for pollock (row 1), cod (row 2), and flounder (row three) +/- median absolute deviation (shaded area) relative to SB40% (dashed line) along projected years over 1000 simulation runs from BRP 0 – 4.

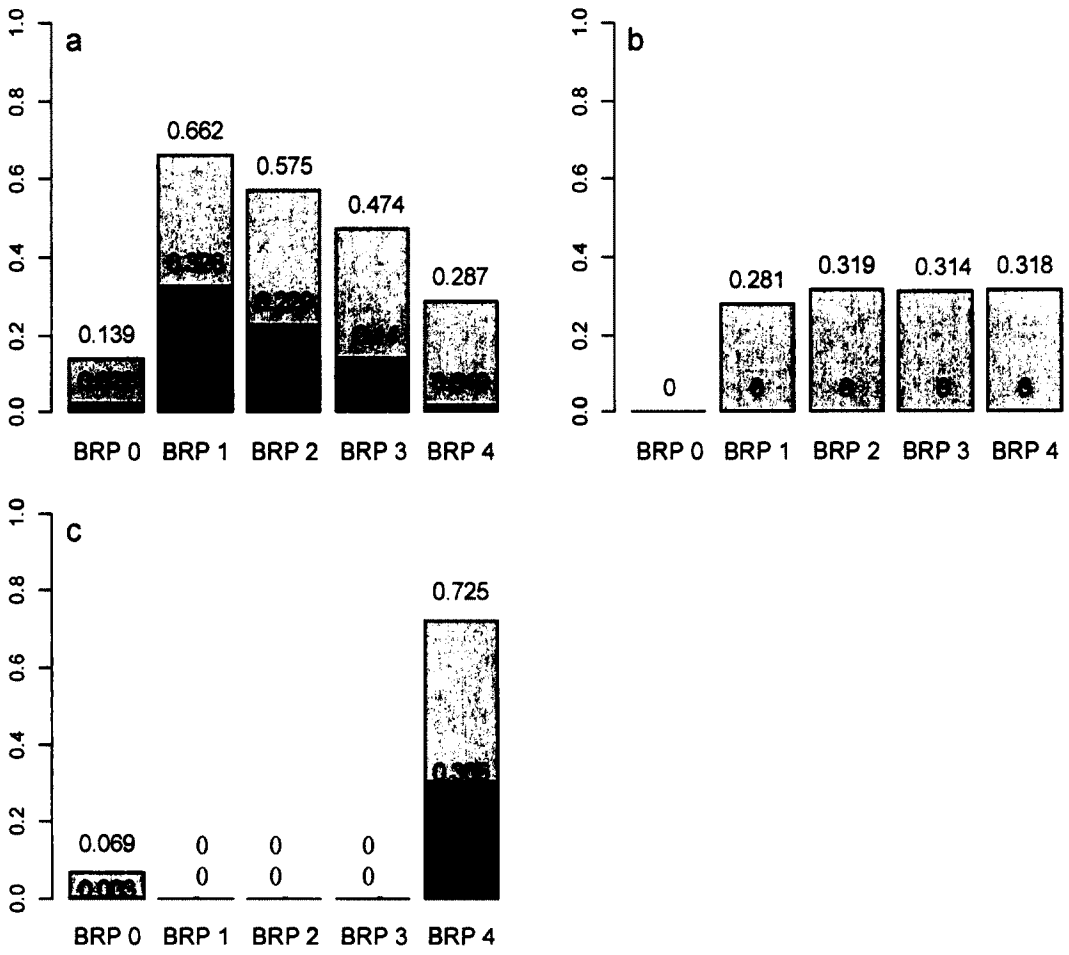

Figure 4.7. Relative proportions of all 50,000 estimates of annual spawning biomass for BRP 0 - 4 (1000 replicates for 50 years each) falling below SB40% (light grey) and SB20% (darker grey) for (a) pollock, (b) cod, and (c) flounder.

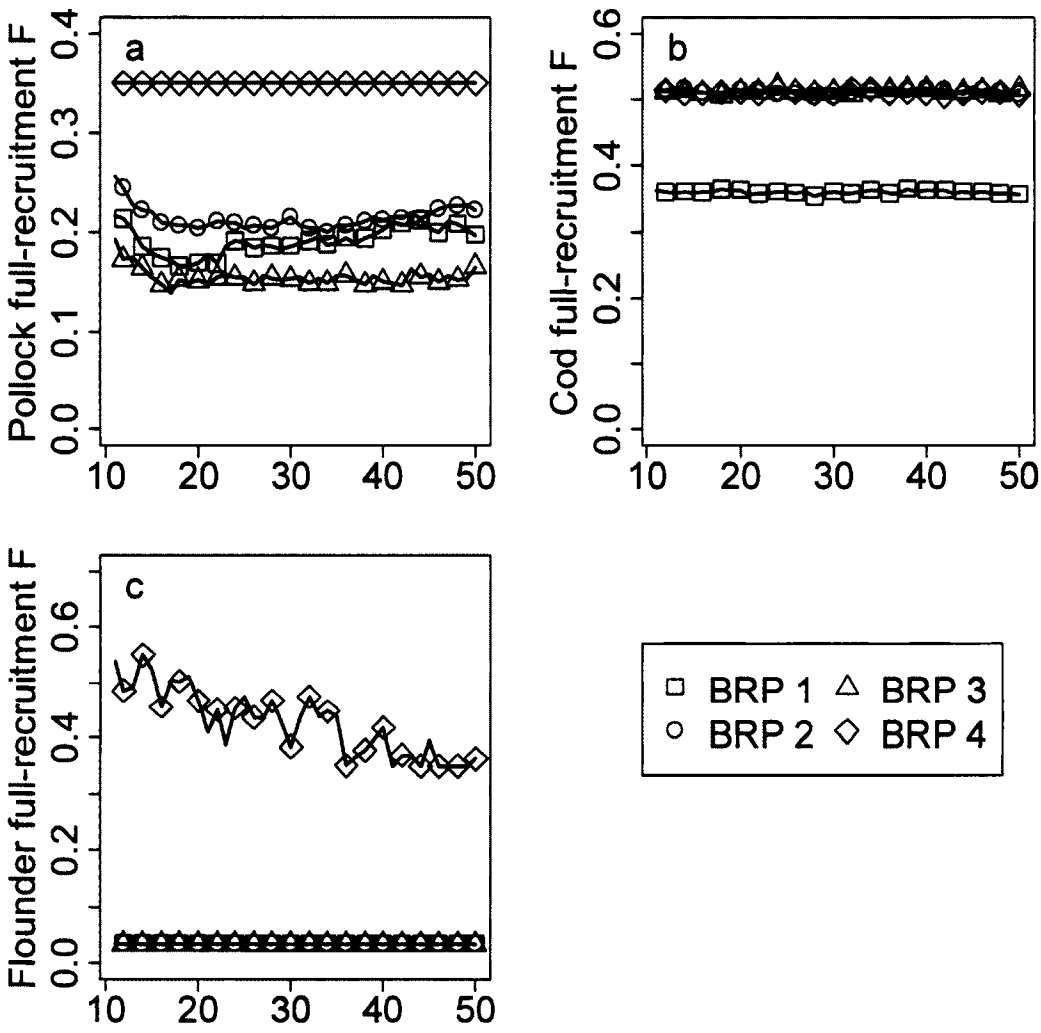

Figure 4.8. Median full-recruitment fishing mortality F for (a) pollock, (b) cod, and (c) flounder for BRP 1 - 4 over 1000 simulation replicates, from years 11 – 50, to eliminate "burn-in" variability from years 1 - 10.

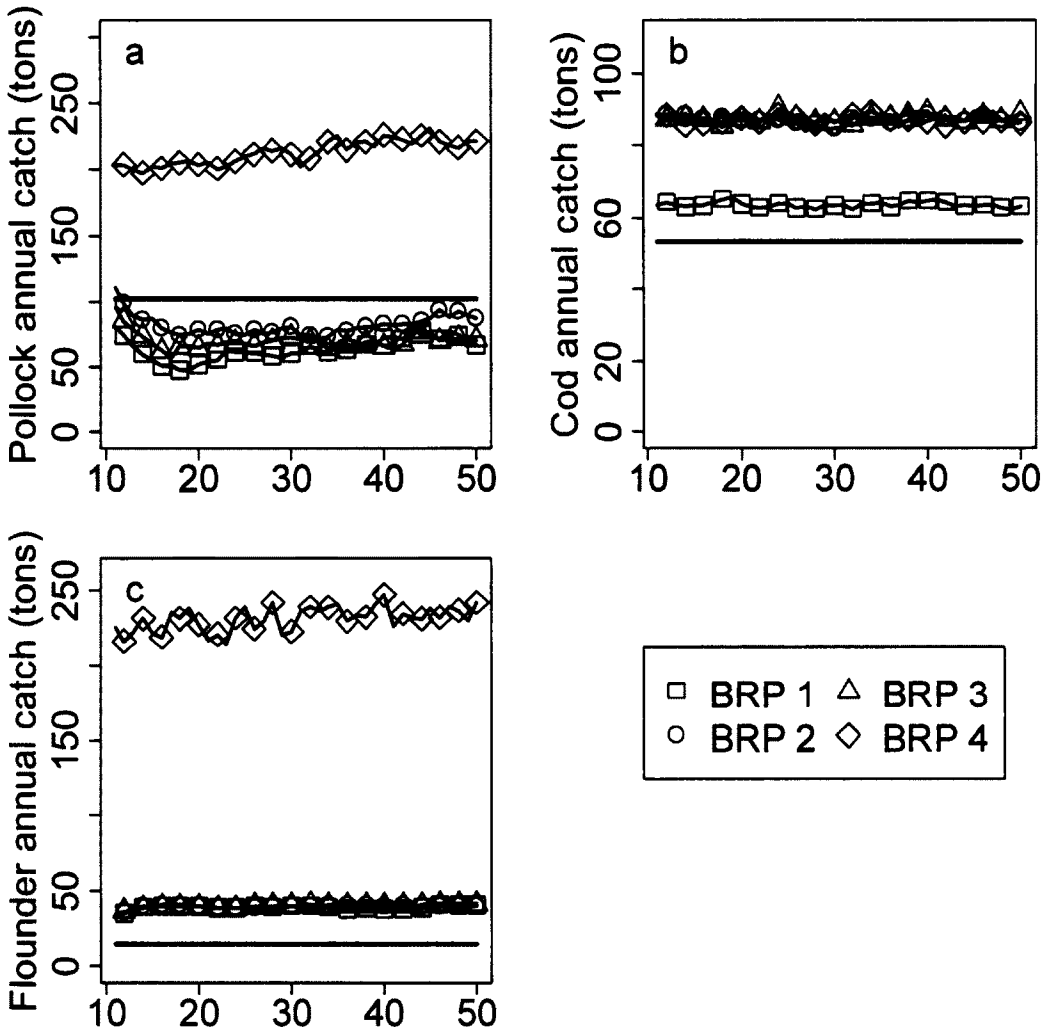

Figure 4.9. Median total annual commercial catch (tons) for (a) pollock, (b) cod, and (c) flounder for BRP 1 - 4 over 1000 simulation runs from years 11 – 50 to eliminate "burn-in" variability from years 1 - 10, compared with mean total annual catch (solid lines) averaged over 1981 – 2010 as per the 2011 AFSC stock assessment.

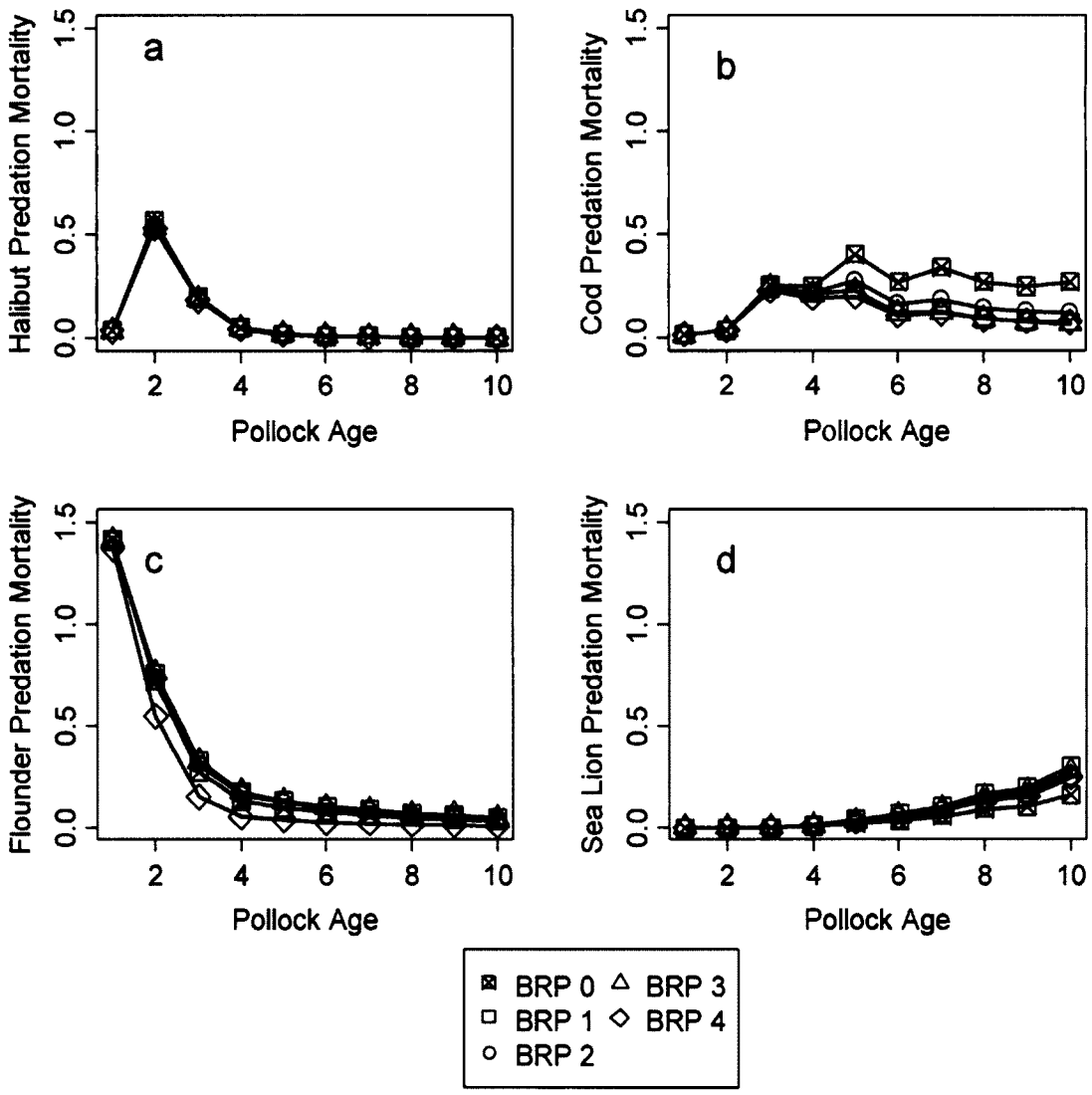

Figure 4.10. Median age-specific predation mortality on pollock from (a) halibut, (b) cod, (c) flounder, and (d) Steller sea lions from BRP 0 - 4.

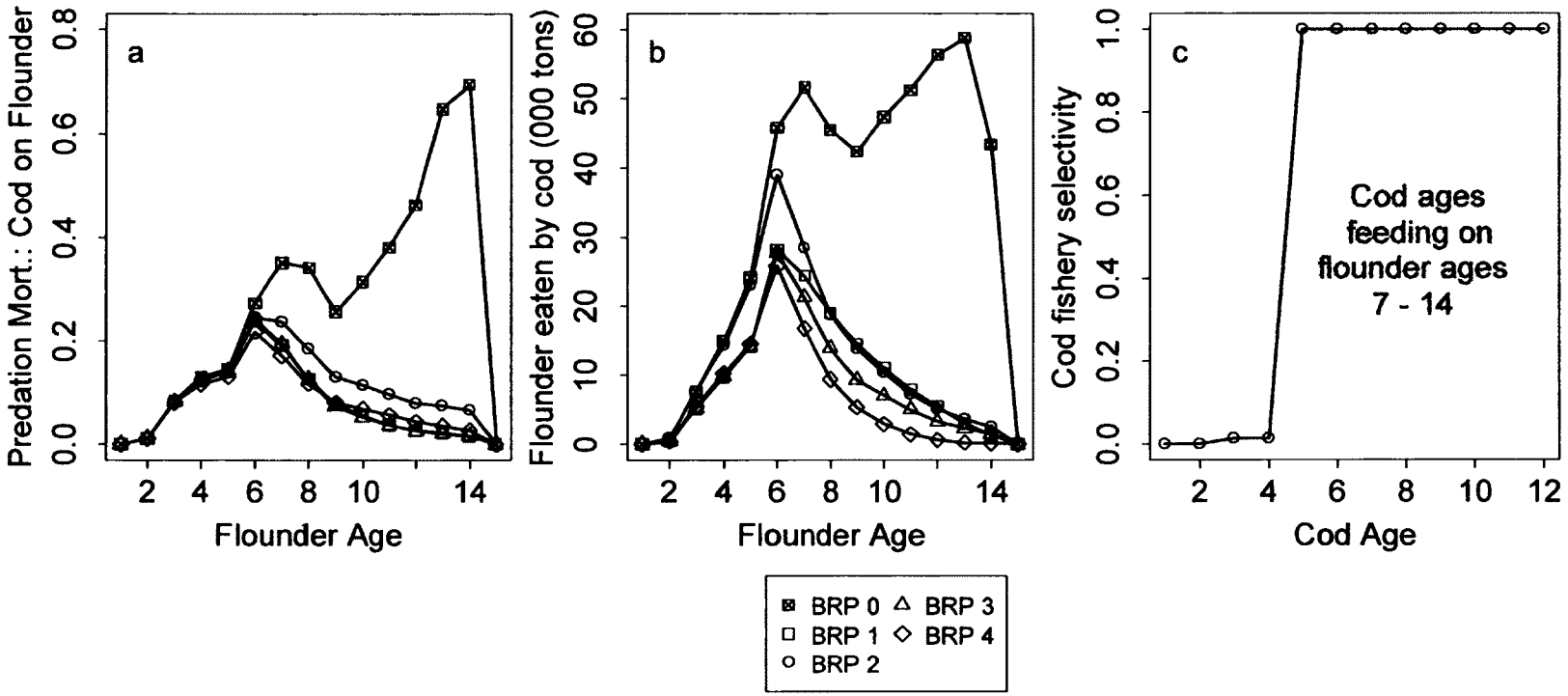

Figure 4.11. Cod-flounder dynamics: (a) median predation mortality from cod feeding on flounder from BRP 0 - 4, (b) median flounder-at-age consumed by cod from BRP 0 - 4, and (c) cod fishery selectivity-at-age relative to cod feeding on flounder ages 7 – 14.

APPENDIX 4A

Data sets and equations for construction of the Gulf of Alaska multispecies age-structured assessment model as per Van Kirk et al. (2010)

Table 4A-1. Population dynamics equations as per Van Kirk et al. [2010] and Quinn and Deriso [1999].

Equation	Description
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}}$	Abundance of species i at age a+1 in year t+1 as a function of abundance at age a and year t.
$N_{i,a+1,t+1} = N_{i,a,t}e^{-Z_{i,a,t}} + N_{i,a+1,t}e^{-Z_{i,a+1,t}}$	Abundance of the plus group of species i at age $a+1$ in year t.
$F_{i,a,t} = s_{f_{i,a}}F_{i,t}$	Fishing mortality of species i at age a in year t.
$C_{i,a,t} = \frac{F_{i,a,t}}{Z_{i,a,t}}e^{-Z_{i,a,t}}N_{i,a,t}.$	Commercial catch-at-age of species i at age a in year t.
$S_{i,a,t} = Q_i s_{s_{i,a}}N_{i,a,t}$	Survey abundance-at-age of species i at age a in year t.
$Z_{i,a,t} = F_{i,a,t} + P_{i,a,t} + M_{0_i}$	Total mortality-at-age Z, the sum of fishing mortality, predation mortality, and residual natural mortality M_0.
Q_i	Survey catchability for species i.
$s_{f_{i,a}}$	Fishery selectivity-at-age for species i at age a
$s_{s_{i,a}}$	Survey selectivity-at-age for species i at age a
$F_{i,t}$	Full-recruitment fishing mortality for species i in year t.

Table 4A-2. Predation equations as per Van Kirk et al. [2010].

Equation	Description
$P_{i,a,t} = \frac{1}{B_{i,a,t}} \sum_j \sum_b I_{j,b} N_{j,b,t} \frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Predation mortality-at-age for prey species i at age a in year t.
$\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}}$	Proportion of prey i,a in all food available to predator j,b in year t, assumed equal to the proportion of food within the stomach of predator j,b in year t composed of prey i,a.
$\phi_{i,a,j,b,t} = v_{i,a,j,b} B_{i,a,t}$	Biomass of prey i,a, in year t multiplied by a suitability coefficient v, which defines the probability of predator j,b, selecting for prey i,a.
$\phi_{j,b,t} = B_{oth} + \sum_i \sum_a v_{i,a,j,b,t} B_{i,a,t}$	Total food available in year t to predator j,b, defined as the sum of all available modeled prey plus a constant "Other Food" term which was set to e^{15}.
$v_{i,a,j,b} = \rho_{i,j} g_{i,a,j,b}$	The product of species-preference ρ, and size-preference g. Size-preference g is temporally constant; species-preference can change relative to pooled stomach data.
$g_{i,a,j,b} = \exp\left[-\frac{1}{2\sigma_j^2} \left(\ln \frac{w_{j,b}}{w_{i,a}} - \eta_j \right)^2 \right]$	Size-preference function for predator j,b. Size-preference is constant over a variety of prey species, but g is prey-specific subscripted as prey species differ in size-at-age.

Table 4A-3. Objective function components as per Van Kirk et al. [2010]. A caret signifies model estimates.

Equation	Description
$\sum_i \sum_t \left[\ln\left(Ctot_{i,t} + 0.001\right) - \ln\left(\hat{C}tot + 0.001\right)\right]^2$	Total catch (lognormal)
$\sum_i \sum_t \left[\ln\left(Stot_{i,t} + 0.001\right) - \ln\left(\hat{S}tot + 0.001\right)\right]^2$	Total survey (lognormal)
$-\sum_i \sum_a \sum_t \left[\left(\frac{C_{i,a,t}}{Ctot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{C}_{i,a,t}}{\hat{C}tot_{i,t}} + 0.0001\right)\right]$	Catch-at-age (multinomial)
$-\sum_i \sum_a \sum_t \left[\left(\frac{S_{i,a,t}}{Stot_{i,t}} + 0.0001\right) * \ln\left(\frac{\hat{S}_{i,a,t}}{\hat{S}tot_{i,t}} + 0.0001\right)\right]$	Survey-at-age (multinomial)
$\sum_i \sum_a \sum_j \sum_b \sum_t \left[\left(\frac{\phi_{i,a,j,b,t}}{\phi_{j,b,t}} + 0.0001\right) - \left(\frac{\hat{\phi}_{i,a,j,b,t}}{\hat{\phi}_{j,b,t}} + 0.0001\right)\right]^2$	Stomach-contents (normal)

GENERAL CONCLUSIONS

The last twenty years of the 20th century have been referred to as "The Golden Age" of fish population dynamics (Quinn 2003), referring to a period in which developments in deterministic modeling merged with advances in statistical methods to produce a plethora of statistically rigorous fisheries population models. This renaissance of fisheries science continues today with a host of approaches for incorporating uncertainty from multiple sources into the modeling of age-structured, temporally variant, and spatially distinct populations.

The challenge facing fisheries modelers today is to expand these approaches to address increasingly complex questions while at the same time preserving the statistical and mathematical foundations that allow for practical and realistic application of their work to fisheries management. The shift towards ecosystem-based management (Marasco et al. 2007) and the desire for a more holistic understanding of the systems affected by commercial fisheries removals have levied demands for data that are often simply unavailable, and the question of minimal complex models that accurately express the desired environmental and biological functions while limiting counterproductive complexity is ongoing.

This study addresses these issues in the context of multispecies model development and prepares the GOA MSASA model for integration into stock assessment efforts. Model development has included considerations regarding the appropriate subset of pollock predators necessary to encompass relevant predation dynamics without loss of

precision or at the expense of excessive variance in parameter estimates (Chapter 1). Simulation exercises (Chapter 2) assessed the impacts of data scarcity and errors in model specification, demonstrating that uncertainty in diet data affects model precision and variability. The impact of such variability, however, can be reduced through objective function weightings and parameter bounds deliberately constructed to allow for flexibility in model performance, especially where such flexibility can be constrained by the influence of more informative data sets such as survey and composition data. The results from Chapter 3 suggest that model structure is robust to the methods used to select annual ration (ingestion rate) for the modeled species, provided that considerations regarding the effects on predation linkages are taken into account. The Type II Holling predator functional response of the GOA MSASA model is more flexible and more sensitive to expressing changes in predator behavior than initially thought, making it an ideal default for the development of more complex responses based on predator influences in a variety of modeling contexts. The model that fitted the data best, however, had a predator response function with competition from predators targeting the same prey (PFR 4).

Chapter 4 applied the refined model to the development of multispecies harvest control rules and biological reference points. Use of current single-species assessments narrowed the buffer between natural variability of populations and the potential for over-fishing, and the construction of multispecies BPRs is clearly warranted. Management strategies that explicitly included species relationships were more successful at maintaining spawning biomass of target species, and such strategies will likely be

specific to the system under consideration. Fishing down arrowtooth flounder in the Gulf of Alaska to allow for pollock increases is an effective harvest strategy, but it is unlikely to be implemented due to bycatch. Similar conditions in other systems, however, may not be subject to similar limitations.

The MSASA model is ideally suited for the complex task of integrating predation into formal stock assessment efforts. It uses many of the same data, is constructed with similar statistical assumptions, and can use disparate weights in the objective function to allow more informative data to reduce uncertainty in the estimation of predation parameters. It is capable of reflecting a variety of predator feeding habits and can be modified along temporal and spatial scales for species-specific application. Estimates of predation mortality-at-age are, of course, highly dependent upon the quality of available diet data; on-going sampling efforts should reduce the uncertainty associated with those data. Continued development and refinement of this modeling approach should prove it to be an effective tool for practical multispecies fisheries management.

LITERATURE CITED

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